publications of the INSTITUTE of MARINE SCIENCE

Volume 8 / November, 1962

Published by the
Institute of Marine Science
The University of Texas
Port Aransas, Texas

In Memoriam

SAM AND JOE GAMPERT

October 1961, after Hurricane Carla. New Research Building and Boat Basin built with $439,000 from The University of Texas, National Institute of Health, and the National Science Foundation.

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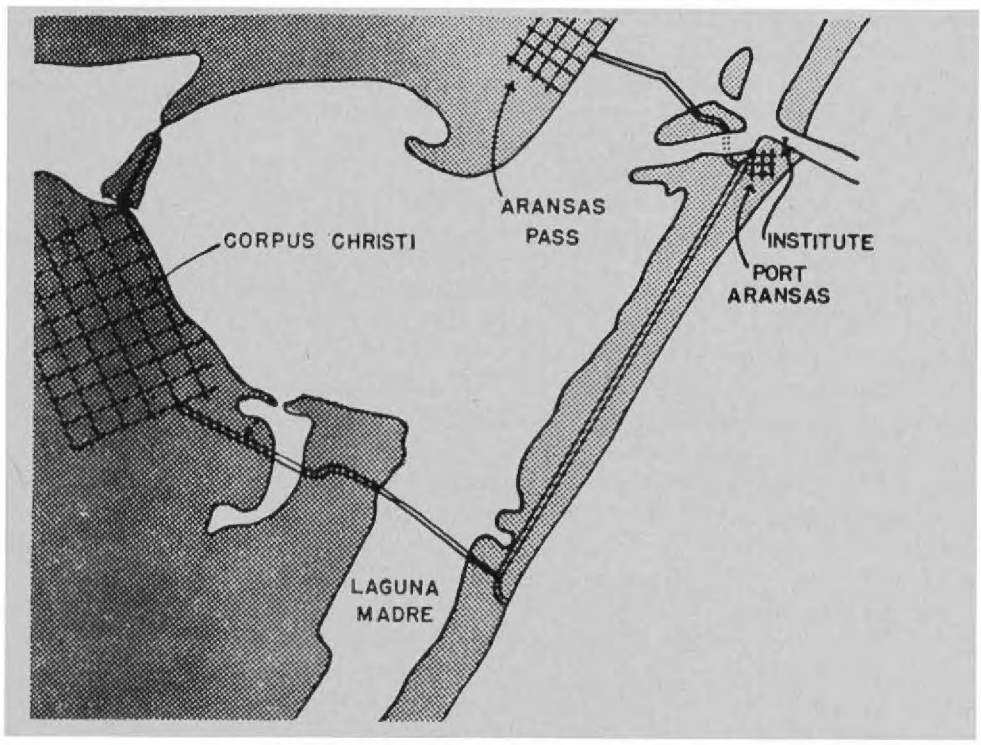

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Fish Production and Biomass Studies in Relation to Photosynthesis in the Laguna Madre of Texas[1,2]

THOMAS R. HELLIER, JR.[3]

Institute of Marine Science and Department of Zoology
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Abstract

The rate of growth of populations of animal consumers depends to a considerable extent on the rate of food supply derived from photosynthetic production of plant material either within the community or that imported into the community. Yet few studies directly relate fish production to plant production. In the present study, an effort has been made to relate fish production to gross plant production in a shallow, frequently hypersaline coastal bay, the Upper Laguna Madre of Texas.

The Upper Laguna Madre is located on the Texas Gulf Coast immediately south of Corpus Christi Bay, and is separated from the Gulf of Mexico by a narrow barrier island, Padre Island.

Biomass estimates of the animal species present were determined with a new population sampling device, the drop-net quadrat. The principle of this method is to instantaneously isolate a segment of the study area with its natural fish population, and by extrapolation determine the approximate density of the fish population of the area. Twenty-nine samples were taken over a 17 month period from March, 1958, to August, 1959.

Age and growth estimates of the dominant fish species were determined by scale analysis, and by reference to length frequency histograms. A total of 31 species were taken during the study, five of which constituted approximately 70 percent of the biomass. These five species were: *Mugil cephalus, Lagodon rhomboides, Leiostomus xanthurus, Anchoa mitchilli,* and *Menidia beryllina.*

Fish production as used in this paper was defined as the weight increase of the fish per unit time while the fish were in the study area. The monthly weight increases for all of the individuals collected during each month were totaled and placed on a per acre basis. Primary gross plant production was measured by the diurnal oxygen method with oxygen samples taken every three hours over a 24 hour period.

Biomass estimates of fish and larger invertebrates ranged from a summer maximum of 337 pounds per acre (37.8 g/m^2) to a winter minimum of 18 pounds per acre (2.0 g/m^2). The annual fish production estimate was 137 pounds per acre (15.4 g/m^2 dry weight) as compared with an annual gross primary plant production estimate of 4177 $g/m^2/yr$ expressed as oxygen. The seasonal migration and growth of fish stocks are in phase with the primary production of food.

Introduction

The rate of growth of populations of animal consumers depends to a considerable extent on the rate of food supply either derived from photosynthetic production of plant material within the community or imported into the community. Yet few studies directly relate fish production to plant production.

[1] From a dissertation presented to the faculty of the Graduate School of The University of Texas in partial fulfillment of the requirements for the degree of Doctor of Philosophy. This study was supported by the Marine Division, Texas Game and Fish Commission through an interagency contract, Dr. H. T. Odum, Principal Investigator.

[2] Contribution No. 55 from the Marine Laboratory, Texas Game and Fish Commission, Rockport, Texas.

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Harvey (1950) in a study of the English Channel and Riley (1955) in Block Island Sound estimated that in terms of carbon content fish use 0.52 to 0.65 per cent and 0.4 to 0.8 per cent of the net phytoplankton production respectively. Harvey's estimates from the English Channel agree well with those given by Riley for Block Island Sound, showing a possible direct relationship between photosynthesis and fish production. A close relation between photosynthesis and growth of juvenile salmon was indicated by Nelson (1958) for a fertilized Alaskan lake. This relationship was evident even though the fish involved was a secondary and tertiary consumer. However, Riley (1955) suggests that the efficiency of conversion of plant material to animal production may vary from one type of habitat to another. For example, brackish coastal waters constitute an environment which favors the dominance of nanoplankton (Ryther, 1954). Riley (1955) suggests that nanoplankton are less efficiently used by large zooplankton and therefore result in a dissipation of available energy by bacteria and microzooplankton.

In general, the shorter the food chain involved, the more efficient is the transfer of photosynthetic products to the higher trophic levels in the community. In a study of fish production on a Bermuda coral reef, Bardach (1959) found a high rate of efficiency of conversion of total solar energy to fish (0.0014%) as compared to that (0.00025%) reported by Clark (1946) for the commercial landings of fishes on George's Bank. The total fish production is probably much greater than the commercial landing. However, even by doubling Clark's efficiency estimate, it is just over a third of Bardach's. Odum and Odum (1955) and Odum, Burkholder and Rivero (1959) showed that utilization of solar energy by reef plants is higher than in many other communities. This high plant efficiency of coral reefs may account, at least in part, for the more efficient conversion of solar energy to fish production in that habitat. Total solar radiation was compared with fish production by Hayne and Ball (1956) in a shallow Michigan pond and the same efficiency value was found (0.0014%) as Bardach presented for a coral reef. Perhaps higher fish production per calorie of solar radiation could be explained by better transmission of light, a higher plant efficiency in very shallow waters, a shorter food chain, or a channeling of solar energy into plant material that is more available to consumers.

Quantitative studies of fish stocks and fish production have not been conducted in bays heretofore because methods were not available. Reliable methods have not been available for measuring the biomass of fishes per area. Most sampling methods are also selective in so far as size of fish is concerned (Carlander, 1956). It usually is most difficult to collect a representative sample of an entire fish population, since different age groups of a species and different species often have different ecological requirements and are not uniformly distributed.

Quite often population and production studies in marine fisheries work are geared to consider only the economically important or easily sampled size ranges of a single species. Some notable exceptions are works by Merriman and Warfel, 1948; Harvey, 1950; and Bardach, 1959. Production studies on marine fishes have been conducted primarily on commercially exploited populations such as the North Sea Haddock, *Gadus aeglefinus*, (Margetts and Holt, 1948). Although this type of study may have considerable value in establishing management policies for a particular fishery, it is difficult to evaluate the ecological economy of the individual species unless its role is known in the overall production of the community.

In the present study an effort has been made to relate fish production to gross plant production in a shallow coastal bay, the Upper Laguna Madre of Texas. The Laguna Madre receives little river water, or water from the open sea, and thus its fish populations are dependent directly or indirectly on plant food produced in the bay. In this study an effort is made to include all of the larger species of consumers. Fortunately, segregation of fishes by size and species in the Upper Laguna Madre is minimized due to the relative homogeneity of the available habitat in the bay.

Description of the Upper Laguna Madre

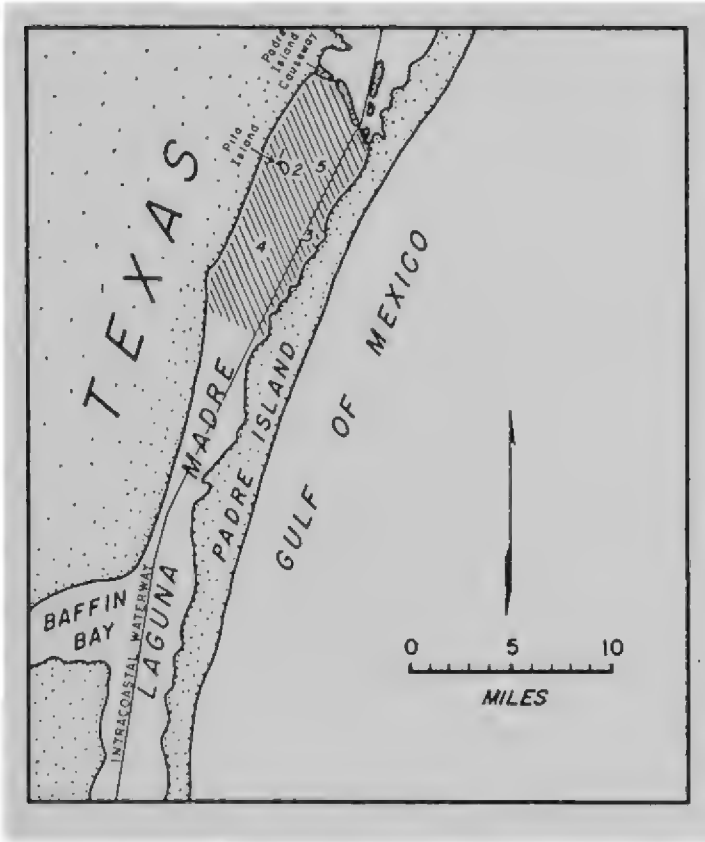

FIG. 1. Map showing sample area (shaded) and principal sample stations. Causeway openings total 1500 feet at normal tide levels.

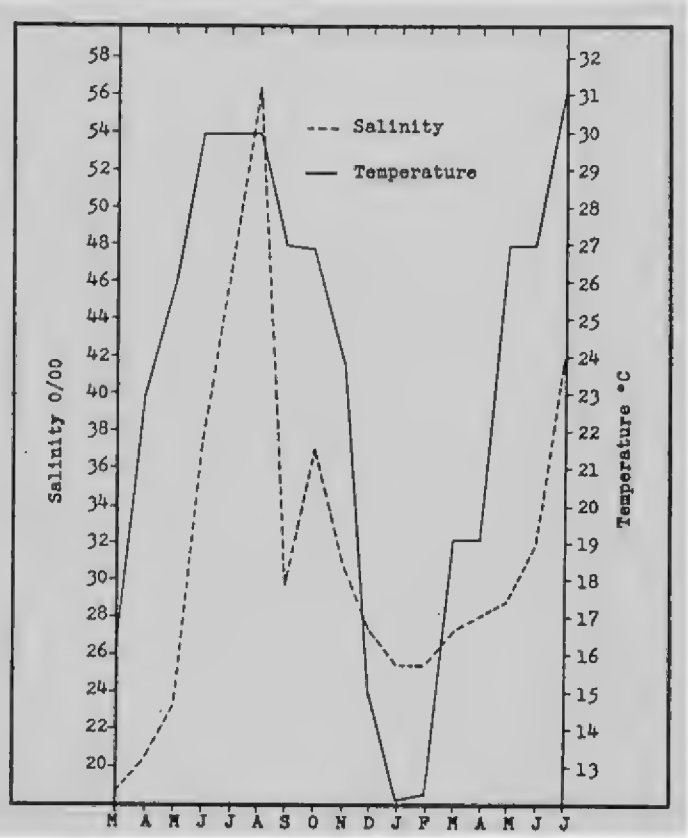

FIG. 2. Average monthly temperature and salinity from the drop-net quadrat in the Upper Laguna Madre, March, 1958–July, 1959.

The Upper Laguna Madre is one of a series of shallow coastal bays located on the Texas Gulf Coast (Fig. 1) immediately south of Corpus Christi Bay. The Padre Island Causeway (a landfill) delimits the northern boundary of the area under study. The Upper Laguna Madre is separated from the Gulf of Mexico by Padre Island, a narrow barrier island, and the southern boundary of the bay is delimited by a semi-dry bar extending from Padre Island to the mainland. This bar is 35 miles south of the Padre Island Causeway. The Upper Laguna Madre is three to five miles wide at mean low tide. A canal, the Intracoastal Waterway, 125 feet wide and 12 feet deep runs north-south bisecting the bay. Spoil banks from this waterway form a nearly continuous island paralleling the canal for 13 miles south of the northern boundary of the bay. From this point south the intracoastal spoil banks are staggered. Water circulation between the Upper Laguna Madre and adjoining bays is limited by the causeway at the northern end which has three openings totaling less than 1,500 feet at normal tide levels, and by the bar at the southern end which has only one opening slightly wider than the Intracoastal Waterway. These constrictions of the bay restrict circulation. In times of low precipitation, a hypersaline condition develops.

A considerable volume of research has been accomplished in the Upper Laguna Madre. The most recent are measurements of community metabolism and chlorophyll by Odum and Hoskin (1958), and Odum, McConnell and Abbott (1958), and an ecological survey by Simmons (1957). Simmons' survey contains a physical and biological description of the area. Hedgpeth (1947) discussed salinities, fish yield, tidal exchange, and pass cutting prior to the dredging of the Intracoastal Waterway in 1948 and construction of the Padre Island Causeway in 1950. He also has listed several organisms from the bay (Hedgpeth, 1953). Gunter (1945a) reviewed attempts to dredge a pass to the Gulf through Padre Island. Salinities over a period of years have been reported by Burr (1930), Baker (1949) and Collier and Hedgpeth (1950). Pearson (1929) worked on the life histories of sciaenid fishes in the area. A general ecological study on Baffin Bay, a tertiary bay opening into the Upper Laguna Madre, 21 miles south of Padre Island Causeway (Fig. 1) was conducted by Breuer (1957).

The northern portion of the bay is very shallow, ranging from one to three feet deep in the zone extending for 13 miles south of the causeway, where there is a natural basin approximately five feet deep. This basin delimits the southern boundary of the present study area (Fig. 1). The shallow portion of the Upper Laguna Madre was covered with a dense growth of shoalgrass (*Diplanthera wrightii*) and widgeongrass (*Ruppia maritima*). *Acetabularia crenulata* was frequently encountered in the area though never abundant. Due to the extreme restriction of water exchange between the Upper Laguna Madre and its neighboring bays no daily lunar tides were perceptible. However, the bay was affected by wind tides and prolonged raising or lowering of the general Gulf tidal level. This long period tidal effect is illustrated by Table 1. This entire northern portion of the bay was extremely homogeneous ecologically, and comprised approximately 27,000 acres.

Five general sampling areas were established in the study area (Fig. 1). Average monthly depths are presented in Table 1, and average monthly salinities and temperatures in Fig. 2.

TABLE 1

Average monthly water depth in meters at station 2

March, 1958	0.33
April	0.41
May	0.91
June	0.76
July	0.66
August	0.63
September	0.81
October	1.23
November	1.00
December	0.66
January, 1959	0.50
February	0.41
March	0.59
April	.....
May	0.89
June	1.00
July	0.69

Material and Methods

Active field work was conducted from March, 1958, through August, 1959. Simultaneous measurements were made of gross photosynthesis, biomass of fishes, and some dominant invertebrates every month.

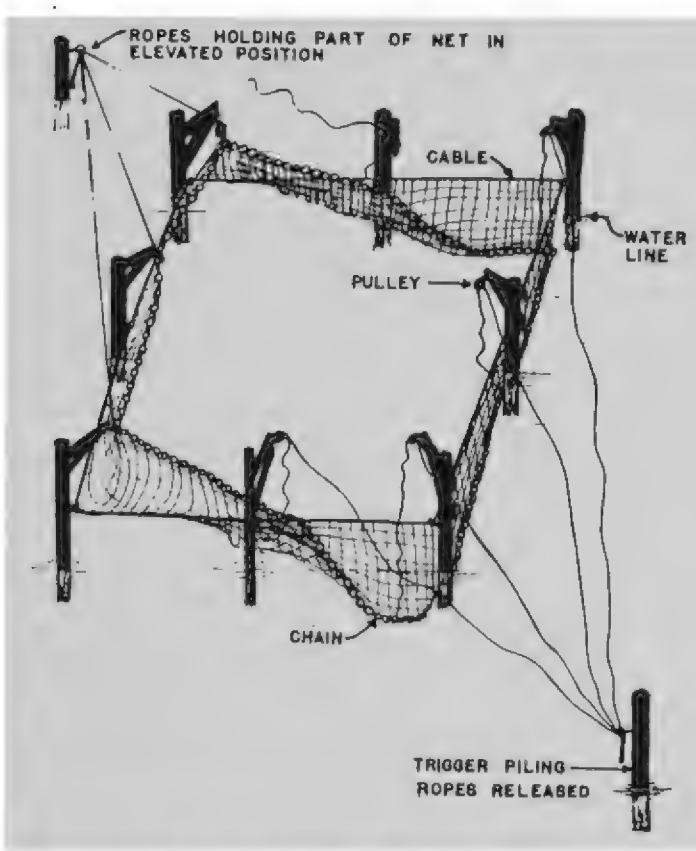

FIG. 3. Drop-Net Quadrat.

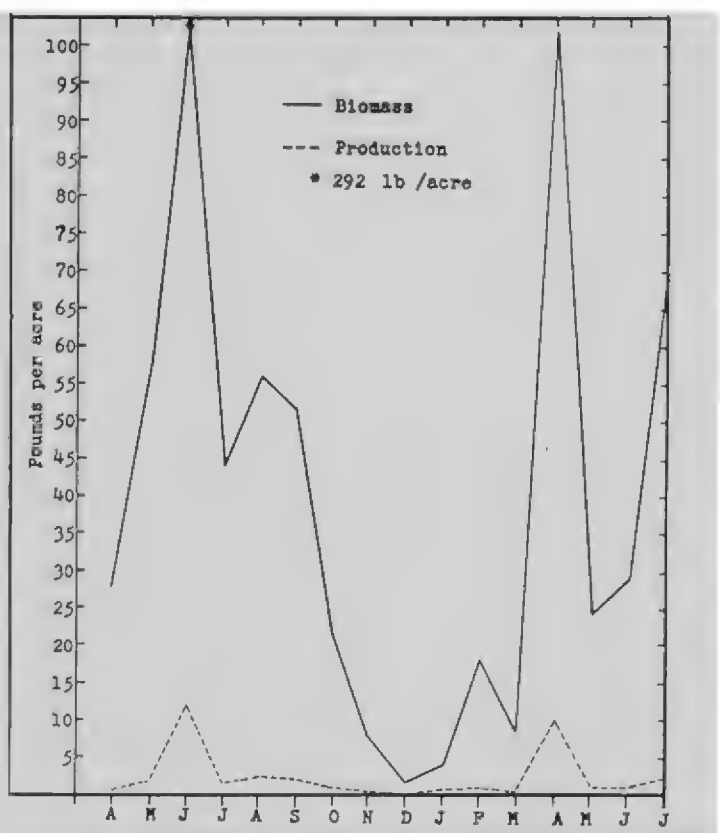

FIG. 4. Biomass and production of the striped mullet, *Mugil cephalus* from the drop-net quadrat in the Upper Laguna Madre, April, 1958—July, 1959. Yearly production may be determined by totaling the production shown for each month.

Biomass estimates were determined with the drop-net quadrat described by Hellier (1959) Fig. 3. The principle of this method is to instantaneously isolate a segment of the study area with its natural fish population and by extrapolation determine the approximate density of the fish population of the area. A description of the drop-net quadrat method of population sampling follows. A quadrat is surrounded with a small mesh net. This net is supported by a steel cable suspended approximately three feet above the surface of the water from eight pilings. A heavy chain (one pound per foot) is used for a lead line on the net. A line is secured to the chain at each piling. These lines are passed through pulleys located on crossarms at the top of the piling, and the net is hoisted clear of the water. After the lines are secured to a trigger mechanism the net is ready to drop.

In the study, quadrats of two sizes were used, one 50 feet square (1/16 acre, 252.9m^2) and the other 100 feet square (¼ acre, 1011.7m^2). The same netting was used on all quadrats. This netting was made of nylon material of number nine thread with ⅜ inch square mesh on an eight foot drop from top to bottom. Care was taken to maintain the netting in perfect repair to assure the retention of all fish. Between six and ten hours were allowed to elapse between the setting and the triggering of the drop-net quadrat. Triggering of the net was always done at night to reduce effects of shadows from the overhanging net.

Fish were removed from the drop-net quadrat by two methods. The larger fish in the quadrat were captured by seining with a 1½ inch square mesh trammel net 300 feet long, and the smaller fish were taken with a 120 foot bag seine of ¼ inch square mesh with a 12 foot bag in the center. Seining was continued in the enclosed quadrat until no more fishes were caught. The number of hauls required to remove the fishes from the quadrat varied from a minimum of five in periods of low population density to 14 in a period of greater density. However, most of the fishes were removed in the first two seine hauls. Table 2 lists the biomass taken per sample.

TABLE 2

Biomass estimates from the drop-net quadrat per sample, compared with some environmental conditions, from March, 1958, to August, 1959

Date	Trap no.	Biomass, pounds per acre			Temp. °C	Sal. ‰	Estimated wind velocity, mph
		Mugil cephalus	Other fishes	Invertebrates			
March 7, 1958	2	.....	31.5	0.3	18.0	22.5	calm
March 14, 1958	2	.....	4.8	0.6	12.0	12.0	20 NW
March 20, 1958	2	.....	7.7	6.5	18.0	19.0	5 ENE
March 28, 1958	2	.....	8.2	9.8	16.5	23.0	10 SE
April 16, 1958	2	28.0	65.8	79.4	21.0	20.5	10 SE
May 22, 1958	2	57.6	100.8	99.6	26.0	23.5	5 NW
June 20, 1958	2	292.0	323.9	12.3	30.0	37.5	20 SE
July 9, 1958	4	41.5	42.2	31.6	30.0	43.0	10 E rain
July 17, 1958	2	86.4	109.3	8.5	30.0	50.0	5 SE
August 10, 1958	3	71.4	110.7	2.6	29.0	56.0	5 SE
August 19, 1958	4	44.2	153.8	5.1	31.0	57.0	15 SE
September 16, 1958	4	86.1	148.6	27.6	28.0	24.5	25 ESE
September 29, 1958	3	17.4	54.9	9.6	26.0	35.0	calm
October 9, 1958	4	46.1	104.9	36.2	28.0	42.0	20 ESE
October 24, 1958	3	0	26.3	0.3	25.5	32.0	calm
November 12, 1958	4	7.0	24.2	4.8	23.8	31.0	10 NE
November 20, 1958	3	6.7	25.1	3.7	21.0	30.0	....
December 5, 1958	4	0	18.5	11.8	16.2	30.0	5 SE
December 10, 1958	3	3.5	19.2	17.5	13.5	25.0	25 NE
January 23, 1959	3	0	3.8	2.0	9.2	24.0	5 NE
January 29, 1959	5	7.5	13.6	16.5	15.0	25.0	calm
February 4, 1959	4	18.5	23.6	0.3	10.0	24.0	5 SE
February 24, 1959	5	18.3	88.9	0.5	14.5	25.0	10 NE
March 10, 1959	3	8.0	56.1	5.9	16.9	27.0	15 E
March 24, 1959	5	7.6	42.0	6.4	19.1	27.5	10 ESE
April 22, 1959	5	101.7	120.8	8.3	19.1	28.0	5 SE
May 25, 1959	4	24.0	41.9	8.1	27.0	29.0	20 SE
June 19, 1959	4	29.0	57.4	17.2	27.0	24.0	10 ESE
July 17, 1959	5	67.8	81.8	4.1	28.0	30.0	15 SE

The reliability of this method is thought to be good in the shallow study area. Samples taken at different stations during periods of stable environmental conditions show a close correspondence as illustrated by the July 7–August 10, 1958 samples and the November samples. The principal sources of variation were sudden environmental changes, which tended to cause the fish to move from the shallow vegetated study area into deeper water, and the intrinsic migrations of the fishes, such as the spawning migrations. The effect of sudden changes in the environment is evident in the July 9, 1958 sample taken during a period of rainy weather, the September 29, 1958 sample following the first sudden temperature drop of the year, and the January 23, 1959 sample made during a period of extreme cold weather. The absence of the breeding population of the striped

mullet is reflected in the late fall, winter, and early spring samples. Migrations of the individual species are discussed under the species headings.

All specimens were preserved in the field in ten per cent formalin. Measurements, weights, and scale samples were taken in the laboratory, and a representative sample of each species was preserved in 40 per cent isopropyl alcohol. Standard lengths and total lengths were measured to the nearest millimeter, and wet weights were taken on a triple beam balance to the nearest tenth of a gram. All length measurements are given here as standard length.

Temperatures were taken to the nearest tenth of a degree centigrade. Depth at the station was estimated to the closest centimeter, and salinity was analyzed to the nearest half of a part per thousand by either a calibrated hydrometer or torsion balance salinometer.

Supplementary collections of fishes were made with the bag seine and with a 16 foot otter trawl having one inch square cod end mesh.

Age and growth of the mullet *Mugil cephalus* were determined by scale analysis. Scales were placed between glass slides, projected in a 2 × 2 inch slide projector, and examined on a screen at a magnification of 18x. Conversion of scale measurements to fish lengths was accomplished with a nomograph similar to that described by Hile (1948).

Estimates of primary production were procured by use of the diurnal oxygen calculation method described by Odum (1956), and Odum and Hoskin (1958). Odum and Hoskin discuss the reliability of this method for the Upper Laguna Madre. Oxygen samples were taken every three hours over a 24 hour period at station two, and analyzed by the Winkler method. A four year record of production in the area is given by Odum and Wilson (1962) in this volume.

Standing Crop and Production of Fish Populations

A total of 31 species of fish was taken in the drop-net quadrat. Five of these species constituted 70 per cent of the fish biomass, and of the remaining 26 species six were not considered resident members of the fish population in the Upper Laguna Madre. Each species is considered separately in order of decreasing abundance.

Mugil cephalus Linnaeus—Striped mullet

Mugil cephalus is one of the most abundant fish in shallow Gulf waters. Gunter (1941) listed it as one of the four most abundant fishes of the Northern Gulf Coast, and Joseph and Yerger (1956) list the mullet as first in terms of species mass for Alligator Harbor, Florida. Thus it was not surprising that the striped mullet maintained the highest biomass of any fish species in the study area.

This species is apparently well adapted for the broad salinity changes in the Upper Laguna Madre. It has been reported from chlorinities of less than ten ppm (Hellier, 1957) and from salinities in excess of 75‰ (Simmons, 1957).

Mullet of zero year class entered the Upper Laguna Madre in January at about 25 mm but at no time during their first year were fish of this group taken in large numbers. It is probable that very small mullet in Texas waters have habitat requirements similar to *Cyprinodon variegatus,* and move into open bay waters only after attaining greater

size. Kilby (1949) describes this type of behavior for small mullet in Florida. Young mullet first entered the drop-net quadrat catch during January at approximately the end of their first year. The mean size of this group was 116 mm. Subsequent age and growth of striped mullet were determined by scale analysis. The validity of this method for *Mugil cephalus* has been shown by Broadhead (1958) in Florida, and by Thompson (1951) in Australia. The mean size at annulus formation for Texas mullet is compared with the data of other authors in Table 3.

TABLE 3

Mean standard length of Texas mullet from scale analysis compared with data of other authors

Area	Age in years						
	1	2	3	4	5	6	7
Texas (present study)	116	181	230	277	324	.....	.....
Texas (Gunter, 1945b)*	81–117	.....	.....	.....	.....	.....	.....
Pensacola, Florida (Broadhead, 1958)†	122	178	226	.....	.....	.....	.....
Homosassa, Florida (Broadhead, 1958)†	153	231	274	314	.....	.....	.....
Georgia (Anderson, 1958)	160	.....	.....	.....	.....	.....	.....
Australia (Thompson, 1954)†	121	203	282	342	398	430	474

* Converted to standard length using 0.79 times total length.
† Converted to standard length using 0.86 times fork length.

Production estimates for this species in the Upper Laguna Madre (Fig. 4) are based on the average monthly growth of the individual fish taken in the drop-net quadrat. Striped mullet in the Upper Laguna Madre show a mean weight increase of 31 gm for the first year, 84 gm for the second, 116 gm for the third, and 167 gm for the fourth. No estimate of mortality, emigration, or immigration was made. However, the effects of these phenomena in the production estimates are minimized by the use of monthly rather than annual production computations. Lengths may be converted to weight by the following length weight equation.

$$\text{Log } W = -4.54 + 2.92 \text{ Log } L$$

Where W = weight in grams

L = standard length in mm

Thompson (1954) summarized a number of food studies on *Mugil cephalus*. These studies indicate that striped mullet are primarily herbivores. A recent study by Darnell (1959) in Lake Ponchartrain shows the striped mullet to be iliophagous.

Lagodon rhomboides (LINNAEUS)–PINFISH

Biomass estimates indicate that pinfish were the second most abundant fish in the Upper Laguna Madre. *Lagodon rhomboides* is one of the most ubiquitous fish in shallow marine water and has been taken abundantly in salinities as low as 1.05‰ (McLane, 1955) and as high as 75‰ (Simmons, 1957). Gunter (1945b) gave a temperature range for Texas pinfish from 9.1° to 34.9°C. During the present study this species was found to be quite active in the Laguna Madre at a temperature of 7.6°C.

Young pinfish appeared in the shallow waters of the Upper Laguna Madre during March or April at a mean length of 25 mm (Fig. 5). The numbers of young pinfish continued to increase in the sample area through June, and then began to decline (Fig. 6). Assuming that sampling was random, this decline indicates emigration and

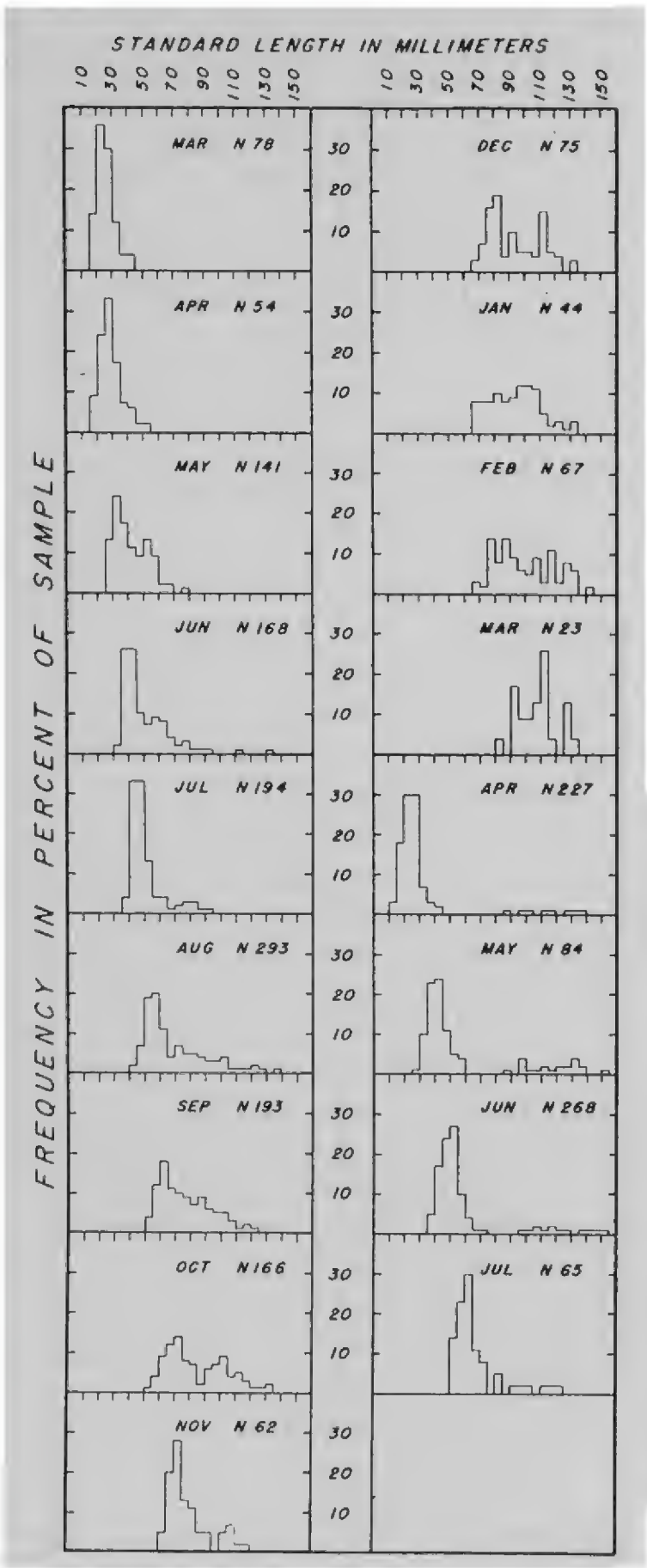

FIG. 5. Length frequency of *Lagodon rhomboides* from the drop-net quadrat in the Laguna Madre, March, 1958–July, 1959.

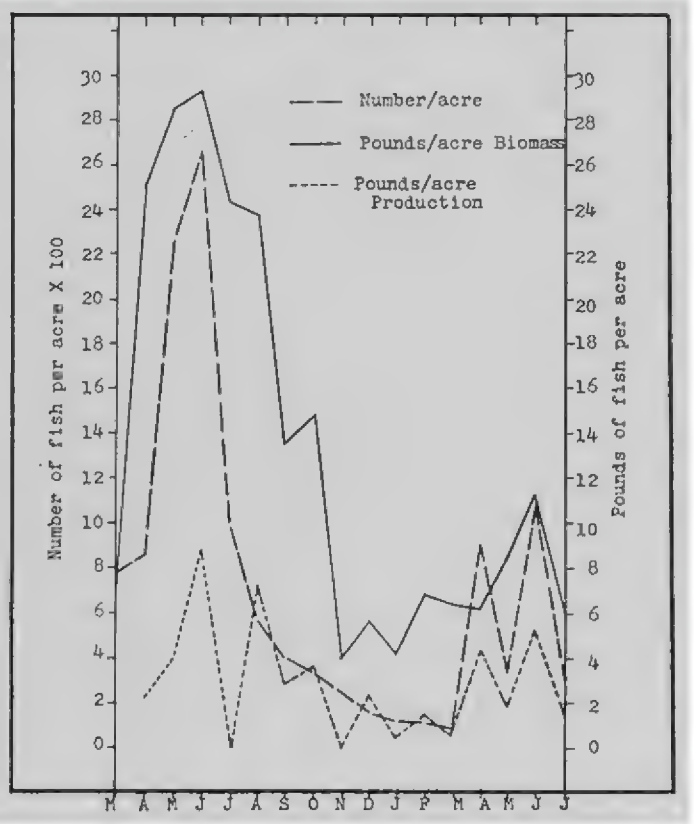
Number/acre
Pounds/acre Biomass
Pounds/acre Production
Number of fish per acre X 100
Pounds of fish per acre
M A M J J A S O N D J F M A M J J

FIG. 6. Biomass, production, and number of *Lagodon rhomboides* from drop-net quadrat in Laguna Madre, March, 1958–July, 1959. Yearly production may be determined by totaling the production shown for each month.

mortality for the population of the area. It is interesting to note that only 4.8 per cent of the June population were found in the area in February. If a similar number of fish were removed from the population in April and in May as in June, no more than two per cent survived until February.

Very few pinfish in the second year class were found in the shallow vegetated sample areas, but supplementary trawl hauls in the channels and boat basins of the Upper La-

guna Madre yielded moderate numbers of larger fish throughout the year. Caldwell (1957) states that *Lagodon* evidently spawns in the open ocean, and Hildebrand and Cable (1938) suggest that this species matures in its second year. It is possible that a majority of the second year fish leave the study area and move toward the Gulf, or into deeper bay waters.

Length frequency data from the drop-net quadrat indicate a growth rate for pinfish slightly greater than that given by Caldwell (1957) for Florida, but very similar to rates found by Gunter (1945b) for Texas, and Hildebrand and Cable (1938) for North Carolina. *Lagodon rhomboides* in the Upper Laguna Madre increases from an average of 25 mm in March to an average of 99 mm in February. This involves a weight increase of approximately 27 g per fish or 2.25 g per fish per month. Production estimates were calculated by multiplying the number of fish taken per month (Fig. 6) times the monthly growth rate as taken from the length frequency histogram. Lengths may be converted to weight by using the length weight equation given by Caldwell (1957).

$$\text{Log } W = -4.3734 + 2.9136 \log L$$

Where W = weight in grams

L = standard length in mm

Monthly biomass and production estimates are presented in Fig. 6.

The pinfish evidently occupies more than one trophic level. Literature records as summarized by Caldwell (1957) show the pinfish as apparently completely indiscriminate in food habits, although more animal than plant material was reported, particularly in the smaller fish. A recent food study by Darnell (1959) tends to support the above statement.

Leiostomus xanthurus Lacepede–Spot

The spot was the third most abundant fish taken in terms of biomass during the present study. Ecologically it is well adapted for the Laguna Madre. Reid (1957) observed a marked gradient distribution of young individuals in East Bay, Texas, with the largest concentrations in lower salinity. However, Kilby (1955) and Simmons (1957) indicate that habitat may have a greater influence on young spot than salinity. Dawson (1958) described the spot as extremely euryhaline, and Simmons (1957) reported it as common in the Laguna Madre in salinities up to 60 ‰.

Length frequency curves indicate that young spot enter the catch in the Upper Laguna Madre during March or April at a mean size of 20 mm (Fig. 7). These fish apparently remain on the nursery grounds in the Laguna until their second year. Large spot in the second and third year classes leave the bays in late fall and winter, and move into the Gulf to spawn. A majority of these fish in Texas waters do not survive to re-enter the bays (Pearson, 1929; Gunter, 1945b).

Growth rates for the spot were determined from length frequencies. Growth rates are very similar to those presented by Townsend (1956) and Dawson (1958). Young spot enter the Upper Laguna Madre in March at a mean length of 20 mm. These fish reach a length of approximately 125 mm by the following February and according to Townsend (1956) 150 to 185 mm at the end of the second year. This involves an overall weight gain per fish of 50 to 55 g for the first year in the Laguna or 4.2 g per month, and an average gain for the second year of 85 g or seven grams per month. Production estimates were calculated by multiplying the number of fish taken per month (Table 4)

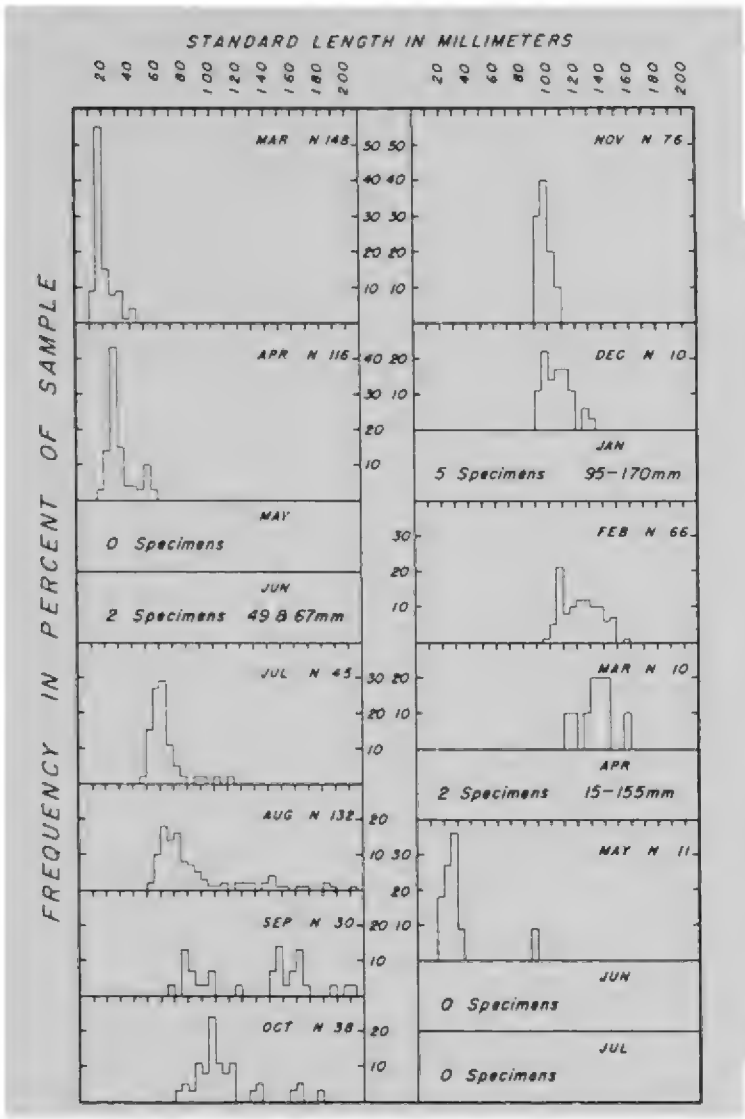

FIG. 7. Length frequency of *Leiostomus xanthurus* from the drop-net quadrat in the Laguna Madre, March, 1958–July, 1959.

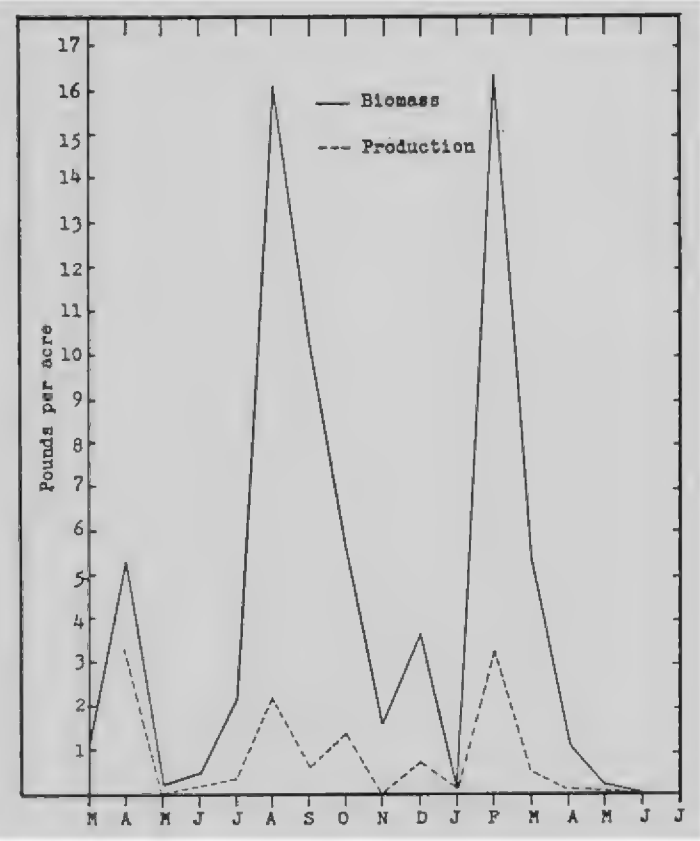

FIG. 8. Biomass and production of *Leiostomus xanthurus* from the drop-net quadrat in the Upper Laguna Madre, March, 1958–July, 1959. Yearly production may be determined by totaling production shown for each month.

TABLE 4

Number of *Leiostomus xanthurus* per acre from the Laguna Madre March, 1958—May, 1959

Month	Number per acre	
	Year class 0	Year class 1
March	1,192	0
April	1,856	0
May	0	0
June	32	0
July	132	0
August	264	34
September	24	34
October	68	8
November	40	0
December	72	0
January	16	4
February	148	116
March	4	36
April	4	4
May	44	0

times the monthly growth rate as taken from the length frequency histogram. Lengths may be converted to weight by using the length weight equation given by Dawson (1958).

$$\text{Log } W = 4.54396 + 2.95831 \text{ Log } L$$

Where W = weight in grams

L = standard length in mm

Monthly biomass and production estimates for *L. xanthurus* in the study area are shown in Fig. 8.

Food studies by many authors as summarized by Dawson (1958) place the spot in a tertiary trophic level feeding on the lower trophic levels such as annelids, ostracods, and copepods.

Anchoa mitchilli diaphana Hildebrand—Bay anchovy

Numerically the bay anchovy was the most abundant species found in the study area, but in biomass it was fourth.

Gunter (1945b) suggests that this species may be more abundant at low salinities although it is euryhaline and very abundant over a wide salinity range. Simmons (1957) encountered *A. mitchilli* at salinities as high as 80‰ in the Upper Laguna Madre.

Very few specimens of this species were taken in the drop-net quadrat during late spring and early summer. The length frequency data obtained from the drop-net quadrat does not allow determination of the spawning season, because the mesh size of the netting retained 25 mm and larger individuals only. However, Gunter (1945b) indicates a prolonged season from spring through fall.

Reid (1956) suggests that at least two age groups are present in East Bay, Texas during June, one group with a mode near 30 mm and another with a mode at 40 mm. It is not possible to separate these age groups during most months from the length frequency data obtained in the present study (Fig. 9). However, a group with a mode at 25 mm entered the catch in March, 1958. This group may represent a late summer or early fall spawning. They reached a length of 32 mm in August and 35 mm in September, which in all probability terminates the first year's growth for the group. This same group reaches 45 mm by the following March and then can be traced no further. These larger *A. mitchilli* left the study area during the summer months either as a result of high spawning mortality or emigration.

The September group averages 0.407 g per individual which represents 0.034 g per month weight increase while the 45 mm group from March averages 1.03 g or a gain of 0.104 g per month. Production estimates for *A. mitchilli* are based on these growth statistics even though growth was probably slightly slower in the winter months and faster during the remainder of the year. Only those specimens large enough to be taken in the drop-net quadrat were considered; consequently, a large part of the first year's growth was not included in the production estimates.

Biomass and production estimates for the bay anchovy are given in Fig. 10.

Reid (1955) states that this species feeds on the lower trophic levels. Darnell (1959) lists zooplankton as the primary food source of this species.

Menidia beryllina peninsulae (Goode and Bean)—Gulf silverside

The silverside is one of the most frequently encountered fish in Texas tidal waters (Gunter, 1945b). However, it was not found to be as abundant in the Upper Laguna Madre during the present study as the larger species, *Lagodon rhomboides* or *Anchoa mitchilli*. Not all of this species were caught in the sampling gear used. *Menidia* below

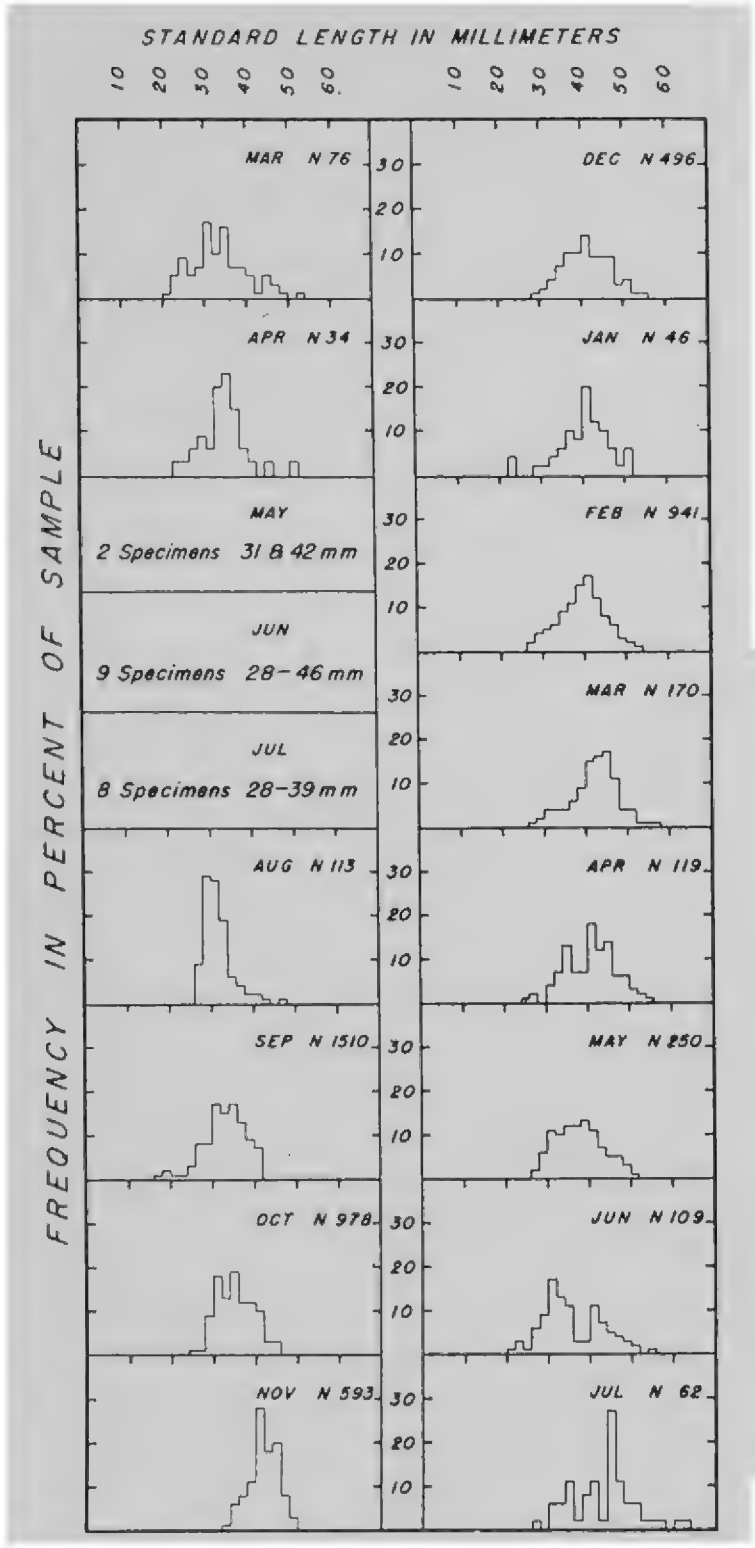

FIG. 9. Length frequency of *Anchoa mitchilli* from the drop-net quadrat in the Laguna Madre, March, 1958–July, 1959.

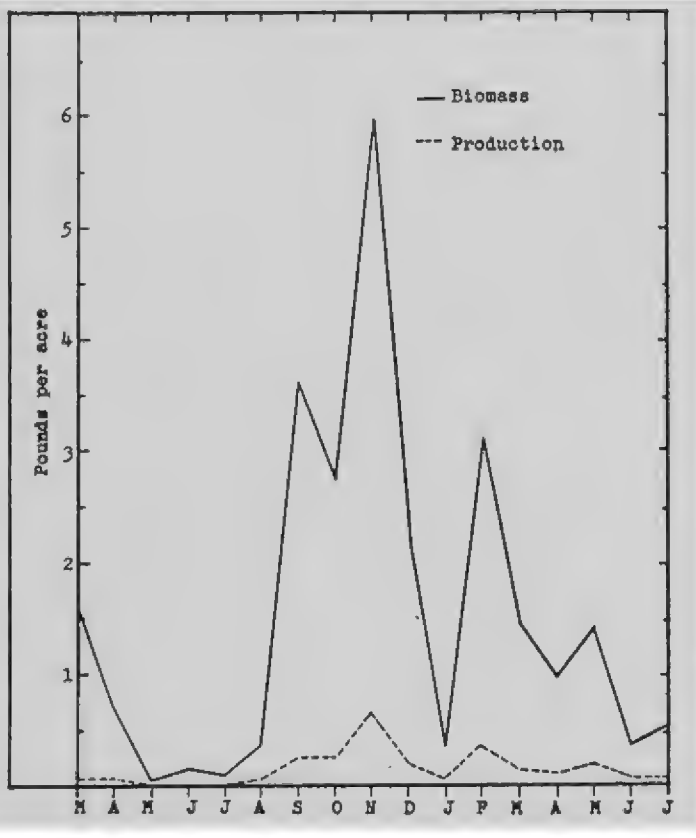

FIG. 10. Biomass and production of *Anchoa mitchilli* from the drop-net quadrat in the Upper Laguna Madre, March, 1958–July, 1959. Yearly production may be determined by totaling production shown for each month.

30 mm were able to pass through the netting of the drop-net quadrat at will and fish from 30 to 35 mm were commonly found stuck in the meshes. The largest biomass of silversides was found during the winter months although this again may have been an artifact of sampling, as the summer and fall populations are composed largely of fish too small to be held by the drop-net quadrat.

The silverside is a fish with a very short life cycle. Bayliff (1950) suggests for *Menidia menidia* that the average life span is only one year. Gunter (1945b) indicates that *Menidia beryllina* does not survive past spawning which takes place at the end of the first year, while Bigelow and Welsh (1925) contend that silversides are probably resident throughout the year wherever found. If this be the case for the Upper Laguna Madre, annual production minus emigration and mortality of silversides should be equal to the biomass of the spawning fish. Simmons (personal communication) states that

Menidia in the Upper Laguna Madre spawn the year round. It has also been shown by Renfro (1958) that this species spawns throughout the year in the Aransas River. There are, however, two spawning peaks, one in late winter and early spring, and another during the summer. A majority of fish over 45 mm standard length were found to be either near or in spawning condition. These larger *Menidia* were considered to represent production in the study area.

Monthly biomass and production estimates are given in Fig. 11, while length frequency data are presented in Fig. 12.

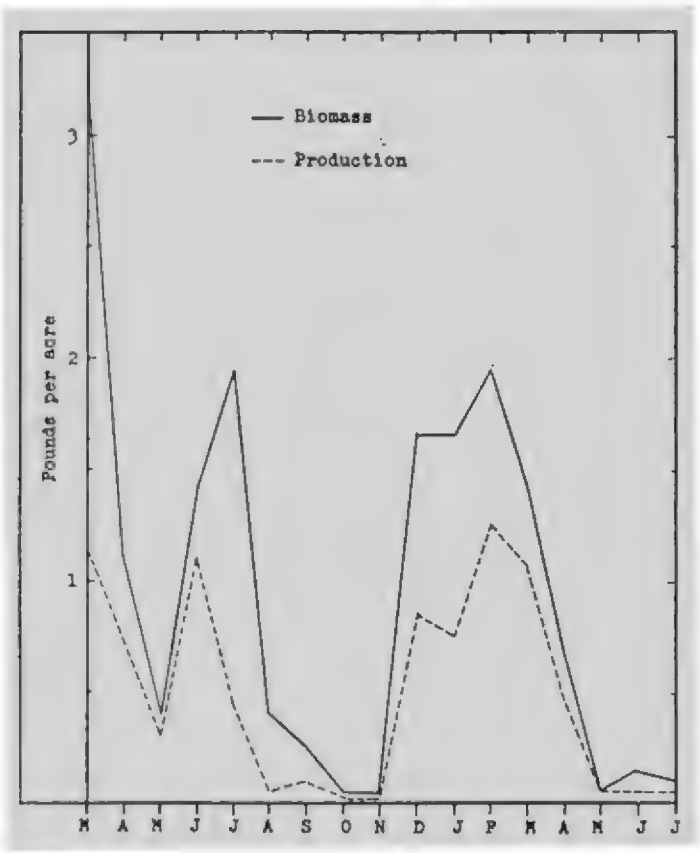

FIG. 11. Biomass and production estimates for *Menidia beryllina* from the drop-net quadrat March, 1958–July, 1959. Yearly production may be determined by totaling production for each month.

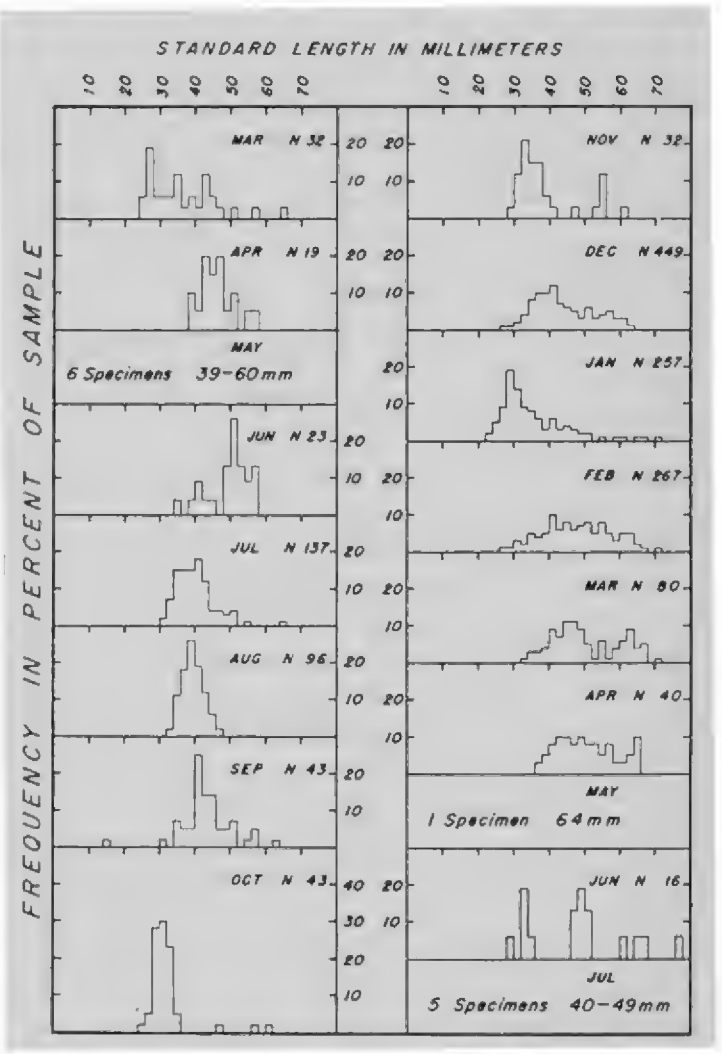

FIG. 12. Length frequency of *Menidia beryllina* from the drop-net quadrat in Laguna Madre, March, 1958–July, 1959.

Kendall (1902) in a rather extensive study described the food of *Menidia* as zooplankton principally, with a few larger animals, diatoms, and unidentified algae. This diet would place the silversides as primarily a secondary consumer.

ANNOTATED LIST OF REMAINING FISHES

Monthly biomass estimates for fish species aside from the five discussed above are given in Table 5.

Many of the species listed were transient members of the Upper Laguna Madre ichthyofauna. Several species, although maintaining resident populations of some magnitude, are so small in the adult form that the collecting method used was ineffective. A few of the listed species were very restricted in habitat preference.

Galeichthys felis (Linnaeus) was taken in some abundance in the shallow grassy study area during the late summer and early fall. Although absent from the collections during

TABLE 5

Monthly biomass estimates from the drop-net quadrat of the least frequently encountered species.*
lb per acre; x indicates less than one tenth of a pound per acre

	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Cynoscion nebulosus	0.2	1.1	11.3	0.1	1.2	4.2	2.4	3.2	0.2	x	....	11.4	20.0	3.8	2.6	3.3	0.2	65.2x
Galeichthys felis	....	....	....	....	....	9.4	11.5	2.0	....	....	....	....	....	1.6	2.1	6.7	....	33.3
Pogonias cromis	....	....	....	....	....	16.0	....	6.1	4.8	....	....	....	....	....	....	....	....	26.9
Bairdiella chrysura	....	....	....	....	0.4	0.9	0.8	1.5	....	....	....	0.1	....	2.6	....	2.4	1.9	10.6
Micropogon undulatus	0.6	3.7	0.9	....	....	1.0	2.0	0.8	....	0.1	x	x	....	x	x	0.4	....	9.5x
Sciaenops ocellata	....	....	....	....	....	1.0	....	....	....	2.2	x	3.8	....	....	....	....	....	7.0x
Brevoortia patronis	....	....	....	0.2	....	....	0.1	4.4	....	0.5	....	....	....	....	x	1.7	....	6.9x
Orthopristes chrysopterus	....	....	0.4	0.3	1.2	0.6	2.0	0.9	....	0.1	....	....	....	....	0.2	0.4	....	6.1

* The following species were also recorded with totals for the 17 months each less than 5 lb per acre. The dissertation (Hellier, 1961) has a record of the weights by month: *Opsanus beta, Paralichthys lethostigma, Anchoa hepsetus, Elops saurus, Cyprinodon variegatus, Trichiurus lepturus, Gobiosoma bosci, Polydactylus octonemus, Hyporhampus unifasciatus, Strongylura marina, Lucania parva, Syngnathus louisianæ, Brevoortia gunteri, Synotus foetens, Paralichthys albiguttus, Sphoeroides nephelus, Syngnathus scovelli, Eucinostomus gula.*

the remainder of the year, rather dense populations were present in the Intracoastal Waterway throughout the spring, summer and fall. Specimens from 91 to 210 millimeters were taken in waters with salinities from 24.5 to 56.8‰ and temperatures from 25.5 to 31 °C. Sea catfish are primarily carnivores preying on crabs and shrimp (Gunter, 1945b).

Elops saurus Linnaeus was taken only during August and September. This species is more frequently encountered in the Upper Laguna Madre south of the area included in this study (Simmons, 1957).

Brevoortia gunteri (Hildebrand) and *Brevoortia patronus* Goode though taken during all seasons were never abundant. Twenty-five millimeter specimens of *B. gunteri* were taken in February.

Menhaden are plankton feeders (Gunter, 1938) feeding on both phytoplankton and zooplankton.

Anchoa hepsetus (Linnaeus) unlike *A. mitchilli* is primarily a Gulf form (Gunter, 1945b). This species was most abundant in the Upper Laguna Madre during the summer. Like *A. mitchilli* specimens smaller than 25 mm could pass through the netting used.

Synodus foetens (Linnaeus) was probably not a resident of the study area, though it was taken in limited numbers.

Cyprinodon variegatus Lacépède undoubtedly maintains a resident population in the Upper Laguna Madre; however, its habitat preference is such as to exclude it from the area of the drop-net quadrat catch. Reid (1954) states that this species at Cedar Key, Florida, was found only in very shallow water around island margins and not in the open waters. Breuer (1957) gives the normal habitat as water less than three inches deep. In the two instances when *C. variegatus* was taken, water temperatures were 16.2 and 9.5°C. Perhaps they moved into the relatively deeper water of the quadrat areas to avoid colder marginal water, a habit suggested for this species by Gunter (1945b).

Lucania parva (Baird and Girard) was relatively abundant during the spring and early summer while salinity was low. Kilby (1955) and Gunter (1945b) indicated that *Lucania* showed affinities for salinities below 15‰. Simmons (1957) does not list this species from the Upper Laguna Madre and it is probable that it is not a permanent member of the ichthyofauna.

Strongylura marina (Walbaum) and *Hyporhamphus unifasciatus* (Ranzani) though taken during late summer and early fall were not abundant and were probably transients in the area.

Syngnathus louisianae (Gunther) and *S. scovelli* (Everman and Kendall) though frequently taken were of a size and shape to pass freely through the netting employed precluding an accurate biomass estimate of pipefish.

Orthopristis chrysopterus (Linnaeus) frequently occurred in samples during spring, summer and fall months, but was never abundant. The pigfish has habitat requirements very similar to those of *Lagodon rhomboides,* and biomass estimates were probably relatively accurate.

Eucinostomus gula (Cuvier) was taken in very limited numbers in late summer and early fall. Simmons (1957) does not list this species from the Upper Laguna Madre, and it is probable that *E. gula* was a transient in the area.

Cynoscion nebulosus (Cuvier) is a highly preferred sports fish on the Texas Coast (Guest and Gunter, 1958), and is very abundant in the Upper Laguna Madre. Simmons

(1957) states that there are two size groups of weakfish in the bay, a group of larger fish of four pounds and over distributed in the deeper water south of the present study area and a group of smaller fish distributed more or less evenly over the bay except during June and July and the winter months when they migrate into deeper waters. This movement was indicated by the biomass estimates also.

Sciaenops ocellata (Linnaeus) shows a size distribution similar to *Cynoscion nebulosus* though they are present throughout the winter (Simmons, 1957).

Pogonias cromis (Linnaeus) according to Simmons (1957) make up over 90 per cent of the sciaenid population over 12 inches long (300 mm). However, again a large majority of this population occurred south of the study area.

Micropogon undulatus (Linnaeus) was present during all seasons though most abundant in spring and early fall. Biomass estimates for this species should be reasonably correct for the period studied.

Bairdiella chrysura (Lacépède) was found by Simmons (1957) to be limited to salinities of 45 ‰ or less. Specimens were taken in the present study from salinities as high as 56.8 ‰ during August at a temperature of 31°C.

Polydactylus octonemus (Girard) was present in drop-net quadrat collections from August and September only. Supplementary trawl samples indicated that this species was present in channels and boat basins from July through November. Simmons (1957) did not list this species from the Upper Laguna Madre.

Trichiurus lepturus (Linnaeus) is common along the Texas Coast (Baughman, 1941), but is not abundant in the Upper Laguna Madre. Gunter (1945b) reported very few specimens from Aransas and Copano Bays, and Simmons (1957) does not list the species from the Upper Laguna Madre. Though cutlassfish were taken in the drop-net quadrat only during September, trawl hauls in channels and boat basins revealed a small population present from March through January.

Sphoeroides nephelus (Goode and Bean) and *Opsanus beta* Goode and Bean are more or less restricted in habitat to oyster reefs, rocks, logs and other obstructions. Very little of this type of habitat occurs in the Upper Laguna Madre; consequently these species were not present in appreciable numbers.

Gobiosoma bosci (Lacépède) was very abundant in the Upper Laguna Madre (Simmons, 1957). However, due to the small size of the adult, no accurate biomass estimates could be made.

Paralichthys albiguttus Jordan and Gilbert was taken only once during this study. Hildebrand (1954) lists this flounder as not too abundant in Texas waters. It is probable that this species is transient in the Upper Laguna Madre.

Paralichthys lethostigma Jordan and Gilbert is the principal flounder taken in the commercial catch of Texas (Ginsburg, 1952). This flounder, as well as *P. albiguttus*, was most often taken by sport fishermen in the Upper Laguna Madre along the edges of the Intracoastal Waterway, and was not found to be abundant in the shallow study area. It was collected during all seasons except summer when it may have been limited by high salinity (Simmons, 1957).

Production of Fishes

Fish production as used in this paper may be defined as the weight increase of the fish per unit time while the fish were in the study area. The method used to calculate

this weight increase for each species considered is included in the discussions of the individual species. The monthly weight increases for all of the individuals collected during each month were totaled and placed on a per acre basis. Growth of four dominant species (in the sense of abundance) in the Upper Laguna Madre has been calculated from drop-net quadrat catches. Little or no fishing mortality existed for these four species in Texas waters. Production estimates were calculated by month from the average biomass present during each month. This tends to minimize the effects of real or apparent mortality on the annual production estimate caused by short term fluctuations in population levels in the area. Replicate biomass samples could not be taken due to lack of time and materials, consequently it would be very difficult to separate sample error from migrations of fishes. It should be emphasized that biomass and production estimates are minimal.

Production of the four dominant species in the Upper Laguna Madre equaled 57 per cent of their highest or summer biomass. This production rate is higher than that found by Bardach (1959) for Bermuda reef fishes. However, Bardach had more long-lived, slow growing species, and he did not include young of the year fish in his growth estimates.

Assuming an average growth rate of 57 per cent per annum for those fishes present in the drop-net quadrat in insufficient numbers for growth calculations, the total annual fish production for the area under study was approximately 137 pounds per acre wet weight (15.4 gm per m^2). Total yearly production for the 27,000 acre study area was 3,699,000 pounds (1,679, 346 kilograms).

Correlations of Fish Biomass and Production to Photosynthesis

The curves in Fig. 13 show a comparison of fish biomass to gross plant production. A correlation between the biomass of fishes present and gross plant production is illustrated by these curves. In examining the curves, one can see a tendency for the biomass of fishes to follow the curve of photosynthesis without much lag during the spring months. This tendency was primarily due to a rapid influx of young of the year fishes. Thus the extreme decline in biomass after the spring peak may at least in part be a function of the availability of food as expressed by the rate of photosynthesis. The biomass is also correlated with the temperature and salinity curves given in Fig. 2. Therefore it is possible that several factors interact to control fish biomass and production. In other years curves of gross photosynthesis were similar although salinity regimes were very different (Odum and Wilson, 1962).

Gross annual photosynthetic production in the Laguna Madre, taken as the area under the curve of photosynthesis in Figure 13 was 4177 $g/m^2/yr$. The annual fish production for the same time interval was 15.4 $g/m^2/yr$ wet weight or 3.1 $g/m^2/yr$ dry weight. The calculated efficiency of conversion of gross plant production into fish production on a dry weight basis would then be 0.074 per cent.

Blue Crabs, Commercial Shrimp and other Invertebrates

Biomass estimates of invertebrates were limited to penaeid shrimp and crabs, and the shrimp estimates must be qualified. Undoubtedly small shrimp were able to pass through the meshes of the drop-net quadrat. The method used was not primarily designed for

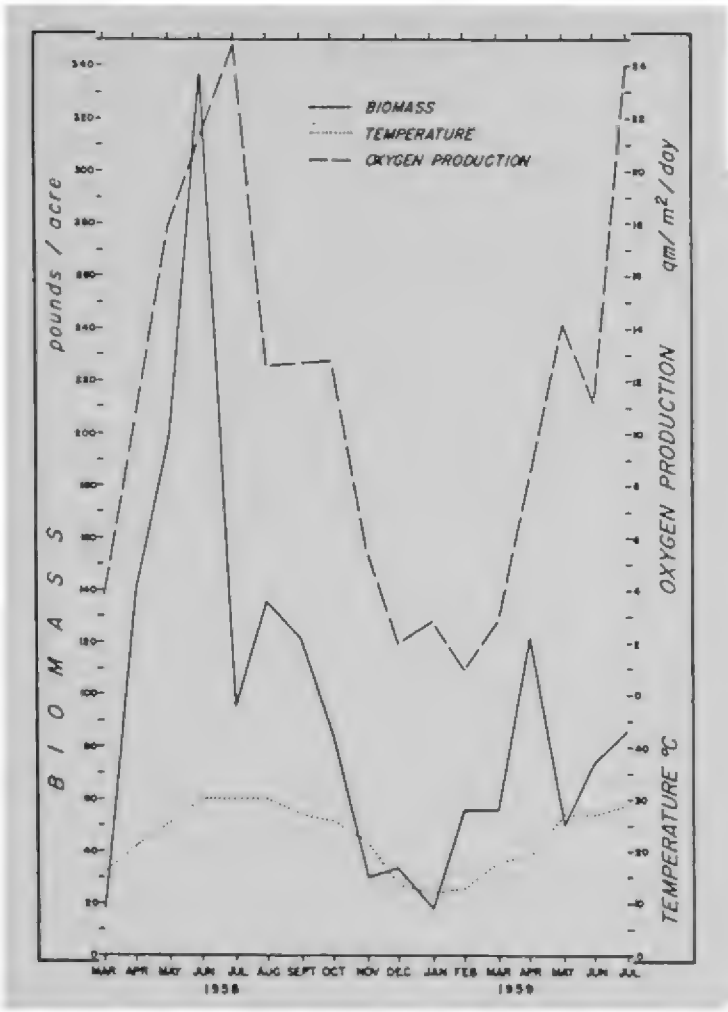

FIG. 13. Total monthly biomass of animals from the drop-net quadrat, compared with gross oxygen production by plants and temperature, March, 1958–July, 1959.

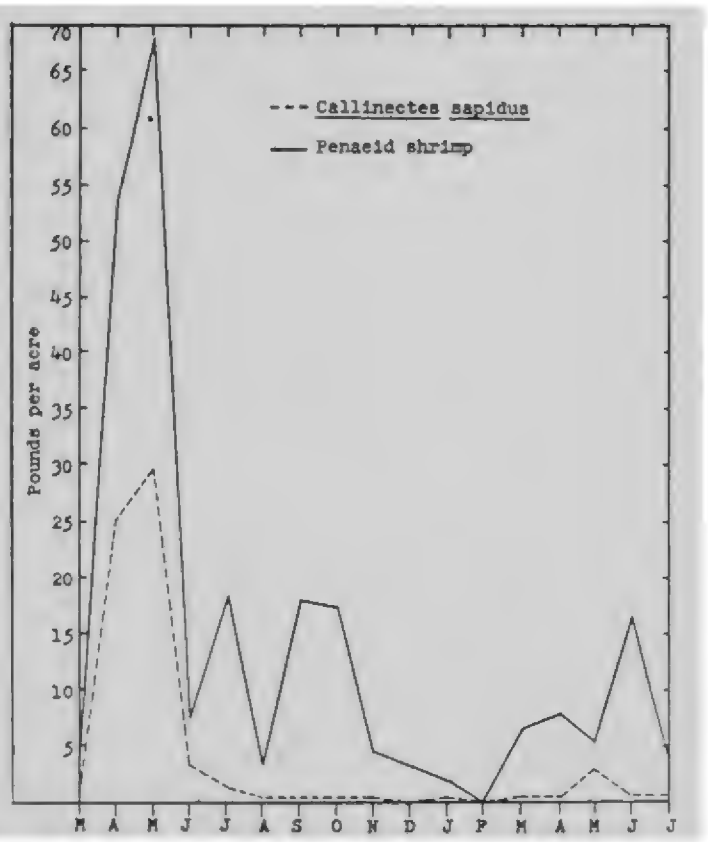

FIG. 14. Biomass estimates of the two principal invertebrates from the quadret drop-net in the Laguna Madre, March, 1958–July, 1959.

a shrimp census. If enough seine hauls had been made to remove all shrimp from the quadrat each collection, the bottom would have almost surely been disturbed beyond immediate recovery; consequently no effort was made to seine to the "last shrimp." However, as with the fish, many of the shrimp were caught in the first seine hauls and relatively few individuals were taken in subsequent hauls.

Three species of penaeid shrimp were present in the drop-net quadrat catch, *Penaeus aztecus* Ives, *P. duorarum* Burkenroad, and *P. setiferus* (Linnaeus). *P. aztecus* constituted a majority of the shrimp catch.

The only species of crab taken was *Callinectes sapidus* Rathbun. Biomass estimates for *C. sapidus* are considered to be relatively accurate as all crabs were easily removed from the quadrat by seining. This crustacean was present in the Upper Laguna Madre during every month, and often constituted an appreciable amount of the biomass. Biomass estimates for the above invertebrates are given in Fig. 14.

Small numbers of *Loligo sp.* were caught in the drop-net quadrat during September, October, and December. This group of invertebrates was not reported from the Upper Laguna Madre by Simmons (1957), and the few individuals captured were probably transient in the area.

No effort was made to estimate populations of Ctenophores or Coelenterates. However, visual observations indicated that these groups were well represented in the study area.

Summary

1. Biomass estimates of fish and larger invertebrates were determined for the upper portion of the Upper Laguna Madre of Texas with a maximum monthly biomass during

the summer of 337 pounds per acre (37.8 g/m^2), and a minimum during the winter of 18 pounds per acre (2.0 g/m^2).

2. Age and growth determinations were made of the four most abundant fish species, *Mugil cephalus, Lagodon rhomboides, Leiostomus xanthurus,* and *Anchoa mitchilli.*

3. The yearly production (total growth of populations during their stay in the area) of all the fishes taken during the study was calculated to be 137 pounds per acre (15.4 g/m^2).

4. Primary gross plant production was measured using the diurnal oxygen method, and is compared with total fish and larger invertebrate biomass graphically in Fig. 13. The annual gross plant production was 4177 g/m^2/yr.

5. The efficiency of conversion of gross plant production into fish production on a dry weight basis was calculated to be 0.074 per cent.

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Further Studies on Reaeration and Metabolism of Texas Bays, 1958-1960[1]

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Abstract

123 diurnal curves of oxygen were obtained in 1959–60 to further outline the patterns of total photosynthesis and community metabolism of Texas bays. Examples were analyzed with nighttime variations in respiration, with changing reaeration constants, and with post-sunset artifacts in computational graphs. The area-based reaeration constant increased with depth, but the volume based reaeration coefficient was more constant at about 1.2 ppm per hr per 100% deficit. The volume-based constant increased with wind velocity. Peaks in the 4 yr seasonal pattern of metabolism in the grassy upper Laguna Madre were in phase with peaks of insolation with P and R remaining in relatively close balance from 0.5 gm/m^2/day in winter to 20 gm/m^2/day in summer. Planktonic systems of Corpus Christi bay were equally productive. Metabolism was slight in a winter cold regime and momentarily interrupted in a spring squall line passage. Hexadecanol had little effect on a salt pond, and inorganic fertilization caused increased metabolism temporarily. Metabolism during dredging was unbalanced towards respiration, and a case of high photosynthesis in flood regimes was reported. A very large diurnal oxygen range was reported in an algal film system with anaerobic nighttime conditions associated with blue-green dominants. Maximum production rates (30–40 gm/m^2/day) were found in the clearest bay, the lower Laguna Madre, with values similar to those for some Texas sewage ponds indicating the effectiveness of natural, stabilized communities in recycling nutrients. Production measurements inside and outside of enclosures indicated the ability of turtle grass systems to maintain fairly normal metabolism for weeks following enclosure. Data from a Louisiana Bayou were similar to data from turbid bays of East Texas. Total phosphorus data indicated slightly higher values in hypersaline bays (2–4 mg-atom/m^3) than in bays flushed with fresh water (0.8–2.4 mg-atom/m^3). The larger bays were equally or more productive than the small sheltered sloughs and harbors of similar depth. Metabolism fluctuated from day to day in a small boat harbor, but conditions remained aerobic. Extinction coefficients were obtained for white light ranging from values typical of Gulf coastal water to those with a 1% compensation point at 0.5 m in turbid bays. Productivities during the summer in the various bays were correlated with clarity. Respiration often exceeded photosynthesis in the back bays where land run-off was more important. For maintaining maximum gross photosynthesis, management measures may be designed for obtaining water clarity and maximum light utilization, for holding stable salinity and nutrient water mass regimes, for conserving well developed bottom communities for holding nutrient cycles, and for controlling bottom depths to intermediate levels (1–2 m) for optimum combinations of light, circulation, and oxygen range.

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Introduction

The bays and estuaries along the ocean margins of the world are the frontiers where man's enterprise is now exploring new ways of using the sea. To carry out research, evaluate fertility, appraise pollution, predict biological events, manage production, develop resource yields, and farm the vast shallow oceans, one must be able to assay day by day the total photosynthesis and respiratory consumption of these ecosystems. Such assay is attempted with the diurnal curve method involving the measurement of oxygen, total carbon dioxide, and other metabolically active constituents through twenty-four hour periods. From such measurements one may seek to compute rates of turnover of chemical cycles, rates of uptake of radioactive substances, productivities, potentials for increased yields of marine products, and metabolic conditions of the bay systems.

In previous papers on the broad, fertile bays of Texas, data were presented indicating the suitability of the diurnal curve method for the determination of gross photosynthesis and total community respiration in Texas waters (Odum and Hoskin, 1959; Park, Hood, and Odum 1958; Bruce and Hood, 1959; Odum, 1960). To further elucidate the nature of total metabolism and reaeration in marine coastal ecosystems, 123 more diurnal curve measurements have been made in special situations, new areas, seasons, and experimental tests. Selected case histories and seasonal patterns are presented in this report in order to interpret the role of depth, light, temperature, turbidity, nutrients, areas, and agitation on production, respiration, and reaeration.

Methods

Oxygen analyses by the Winkler method were made on water samples collected at frequent intervals through 24-hour periods representing whole functional areas and water masses. Then rates of gross production, respiration, and reaeration were computed. Procedural details on the graphical analysis were presented in a preceding report (Odum and Hoskin, 1958). In other papers variations were described for some special situations (Odum, 1956, 1957, 1960; Odum, Burkholder, and Rivero, 1959). Several new refinements concerning the computation of diffusion and respiration are here described. These methods apply in thoroughly mixing shallow waters.

Phosphorus analyses were made by H. Bruce (Bruce and Hood, 1959) and R. Ward working with C. Oppenheimer using perchloric acid digestions followed by stannous-chloride-ammonium molybdate colorimetry.

Field measurements of foot candles were made with a General Electric Golden Crown Exposure Meter, Type PR 3 with an incident light attachment. The manufacturer supplied a foot candle calibration. Under conditions of rough field use, changing tensions on the spring, and other factors, the foot candle data must be considered approximate and relative.

Wind velocities were measured in the field with a hand anemometer Model MRF Florite from Bacharach Industrial Instrument Company, 200 W. Braddock Ave., Pittsburgh, Pa.

Corrections for Changing Nighttime Respiration

From studies by Beyers (1962) on microcosms, from data in some diurnal curves (Fig. 1 and 2), from diurnal data in Silver Springs (Odum, 1957), and from experiments on plant respiration as a function of oxygen content by Gessner and Pannier (1958) it is known that the respiration of oxygen after dark may exceed that just before dawn in many instances, especially when oxygen content is much higher at sunset than at sunrise. Wherever post-sunset respiration is higher than respiration later at night an error in the diffusion computation may be introduced ultimately causing a slight overestimation of of total community respiration.

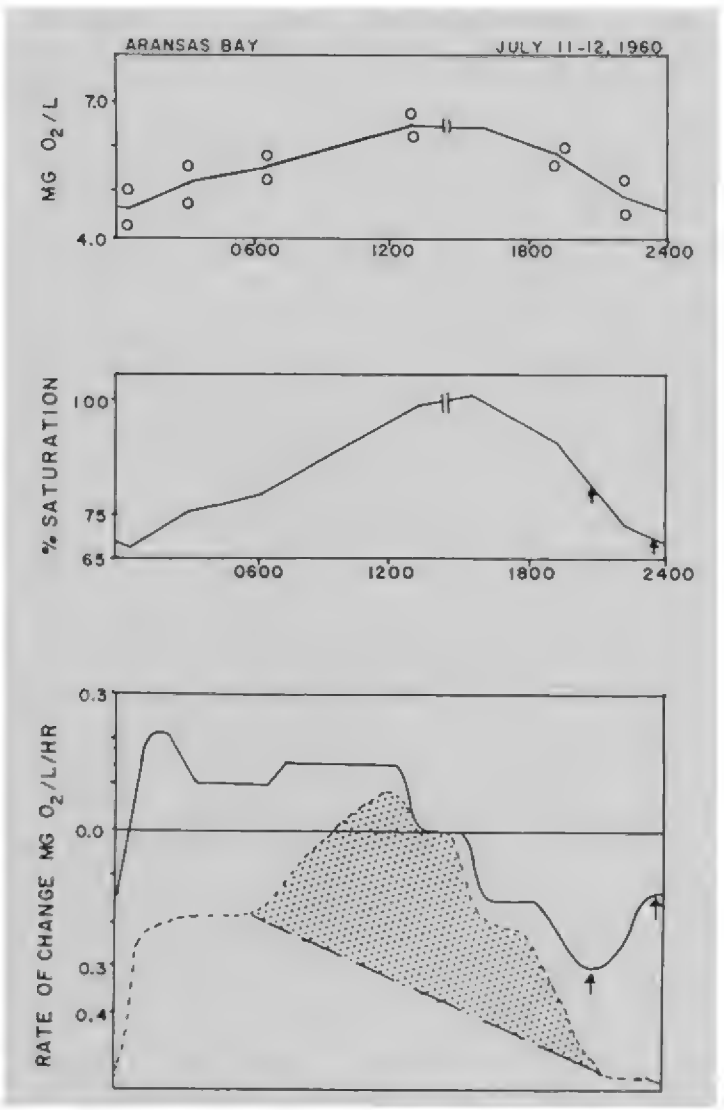

Fig. 1. Diurnal curve off Hunt's Pier, Rockport, Texas, in Aransas Bay, July 11–12, 1960; salinity, 21 ‰. This is an unusual curve in which the respiration decreases markedly during the night. The change in rate of nighttime oxygen decrease occurred even though the winds diminished from 18 mph at sunset to 7 mph at sunrise.

Recalling the procedure previously outlined in detail (Odum and Hoskin, 1958), one selected two points during the night from the rate of change graph. In the routine previously used the respiration was taken to be constant at both times of night and any difference in the rate of oxygen decrease was attributed and computed in ratio to the difference in per cent saturation of the water at the two times. Since both respiration and the tendency for diffusion out are greatest in the early part of the night (or tendency for diffusion inward is minimal), one attributed too much of the observed oxygen

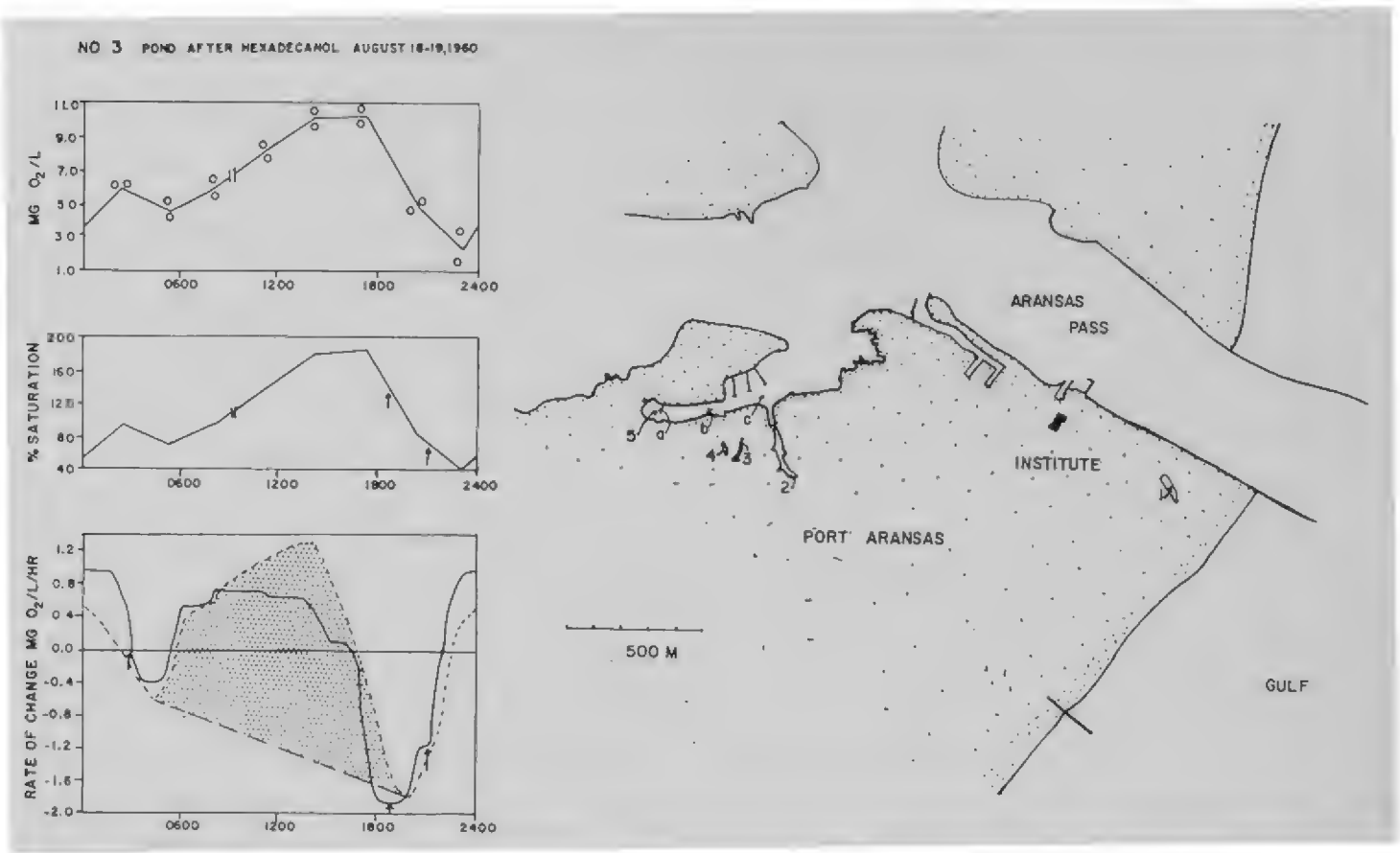

FIG. 2. Diurnal curve in a shallow slough (Pond No. 3) after addition of hexadecanol at noon, Aug. 18–19, 1960: salinity 33.6 ‰; wind with little variation through the night 0–6 mph. This curve shows a decrease in respiration during the night. Also included is a map of Port Aransas waterways showing ponds and sloughs: 1, beach pool; 2, shell shop pond; 3, Oppenheimer House pond; 4, ferry road algal mat; 5, city boat basin, stations a, b, and c.

decline at night to diffusion. The diffusion correction was overestimated. When the graphs were finally completed, the nighttime respiration was slightly overestimated and the P/R ratio too low.

In aerobic waters the magnitude of error is small judging by the small differences in nighttime oxygen respiration indicated in sources cited above. The large differences in Fig. 1 and 2 are unusual. In anaerobic waters, however, very large differences develop as recently reported (Odum, 1960) in cases in which oxygen consumption although rapid after sunset stops later at night as oxygen runs out. To some extent a localized anaerobic effect may always exist where the bottom ooze is in the euphotic zone with declining oxygen metabolism at night.

Data by Beyers (1962) on carbon metabolism of several types of balanced microcosms show the maximal nocturnal respiration at sunset suggesting a relation to the labile organic matter accumulating from the net production of the previous day. In his graphs respiration declines rapidly, perhaps logarithmically during early night. If the bays are behaving similarly, the diffusion constants obtained in this paper with the simple formula (R constant) are too large, since they include some of the change in respiration as change in diffusion. Were the change in respiration during the night between the two computational times known, the diffusion constant might be used as

$$k = \frac{(q_e - q_m) - (r_e - r_m)}{S_e - S_m}$$

where k is the volume based diffusion constant, q the rate of change, r the respiration, and S the saturation deficit.

Because the data on diurnal pH CO_2 curves for these bays (Park, Hood, and Odum, 1958) do not yet show systematic trends in nighttime respiration, it seems premature to attempt complex assumptions about respiration for estimating diffusion directly from the diurnal graphs. Thus in this paper the simple procedure has still been used, and the values for diffusion constant may be regarded as upper limits. Ultimately independent physical determinations of the reaeration constant may solve this problem with the night respiration and daytime net photosynthesis determined after subtraction of diffusion as independently determined.

In rate graphs analyzed in the previous paper (Odum and Hoskin, 1958), one line for "R" was drawn through the average nighttime respiration. In many of the graphs after diffusion corrections have been applied, there was observed a greater respiration after dark than before dawn even without the correction of the diffusion constant described above. Where pre-sunrise and post-sunset respiration differ in this paper, a dashed line is connected diagonally connecting dawn respiration rate to the sunset respiration rate on the rate of change graph. This line may be used for counting squares in estimating gross photosynthesis. How real the line may be as an indication of daytime respiration is not known.

Where the diurnal variation of respiration of oxygen is severe as in anaerobic systems, it seems best to use a reaeration (diffusion) constant that is approximated independently from k's in similar conditions of depth and mixing as measured under aerobic conditions (Fig. 3). For example, k or about 1 gm/m^3/hr/100% deficit is representative of the Texas bays under average conditions. After applying the assumed diffusion constant, one may use the corrected rate graph to indicate the course of night respiration.

Reaeration Constants and Water Depth

In streams the area-based reaeration coefficient increases with the rate of stirring and thus increases with current, wave action depth, and size of the water eddies (Phelps, 1944; O'Connor, 1958; Velz, 1939). Consider reaeration relationship to depth in the bays. Reaeration constants computed by the diurnal curve method for Texas bays have been plotted in Fig. 3 as a function of depth. Reaeration and the variation in reaeration increase with depth. Although the reaeration computations from diurnal curves are subject to many sources of variation and error, the data show a regression from values of 0.1 gm/m^2/hr/100% deficit in shallow water to values greater than 3 gm/m^2/hr/100% deficit in the deeper bays. The line in Fig. 3 may be used to estimate reaeration constants where night data are inadequate or where other complexities prevent the usual computation.

The volume based reaeration constant (k) in gm/m^3/hr/100% deficit is related to the area based constant (K) by the definition:

$$K = zk \text{ where z is depth in meters.}$$

The regression line for K from Figure 3 was converted into a line for k by dividing by depth as indicated in Fig. 3. The volume based constant is rather independent of depth in these bays.

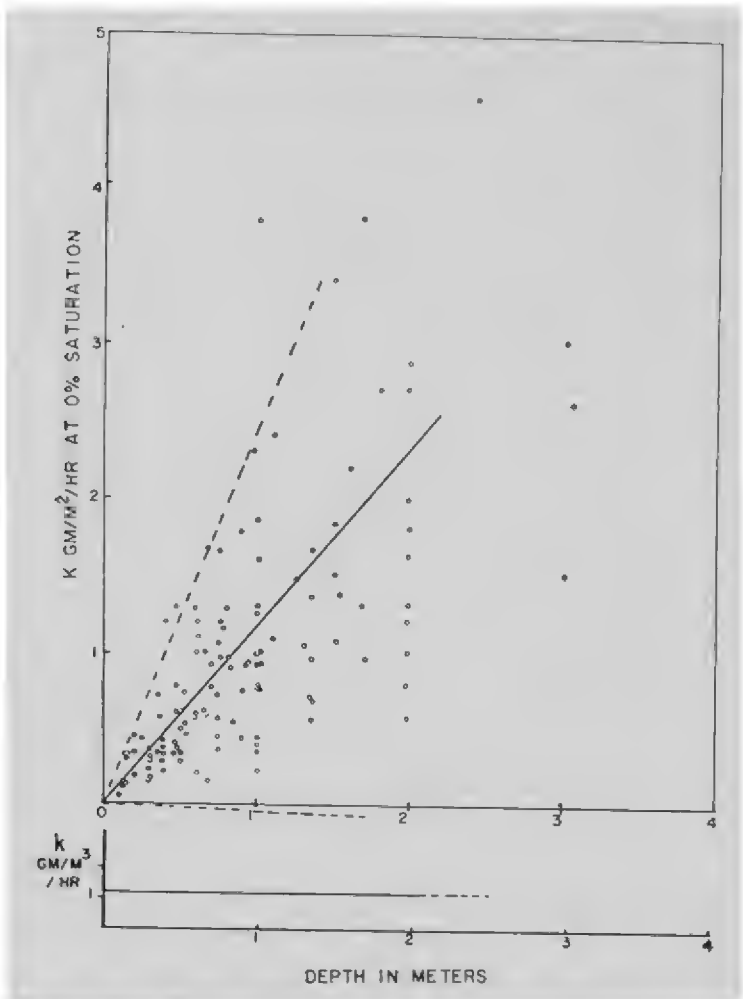

FIG. 3. Reaeration constants on an area basis (K in gm/m²/hr/100% deficit) as a function of the bottom depth (in meters). A linear regression line is plotted as computed from the data points. Dashed lines form boundaries for 95% confidence. Also plotted is the same regression line expressed as a volume basis ($k = K/z$ in units mg/l/hr/100% deficit). Each point in this figure was computed from a diurnal curve using changing rates of change at night following the procedure of Odum and Hoskin (1958).

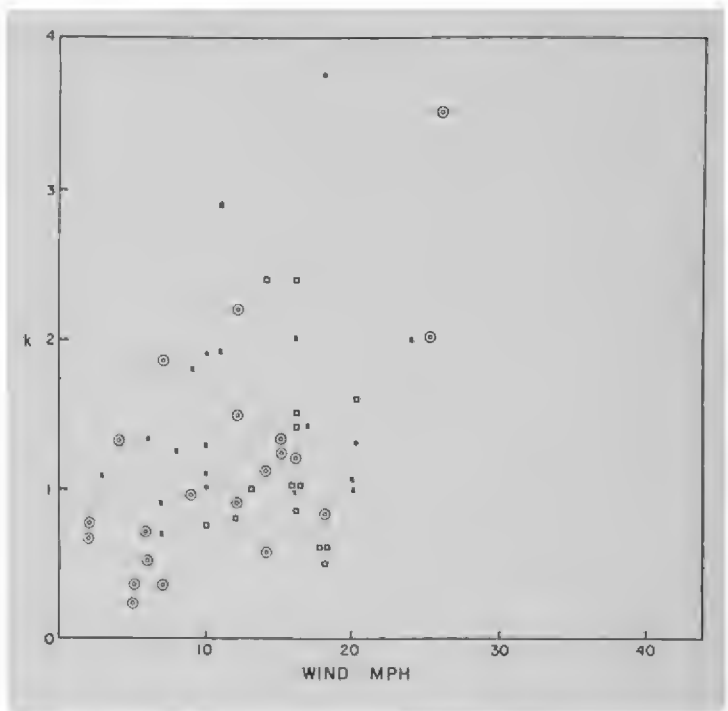

FIG. 4. Reaeration constants on a volume basis (k in units mg/l/hr/100% deficit) plotted as a function of average wind velocity during nighttime hours.

Values for reaeration in San Diego bay of about 0.12 gm/m³/hr/100% deficit (volume base) (O'Connor, 1958) and for the Thames estuary by Gameson and Barrett (1958) of 0.5 gm/m²/hr (area base) are within the range in Texas waters on the low side.

REAERATION CONSTANTS AND WIND VELOCITY

Because the passes are narrow and the Gulf tides small there is little tide in most of the bays and most of the stirring action is wind driven due to waves and wind-induced circulation. The reaeration coefficients as computed from the diurnal graphic analyses are plotted for environments of similar depth in Fig. 4 as a function of observed wind velocity during the night. Increasing reaeration coefficients can be observed with increasing winds. The graph in Fig. 4 has been used in several instances to compute diffusion corrections on days in which wind velocities varied markedly at different times. Estimates of wind velocity in the field were used to select a reaeration constant for each time of the day. Computation of reaeration rates from a diurnal graph can only be done if one has two periods with nighttime rate measurements in which wind velocities are fairly similar. Such data are plotted in Fig. 3 and 4.

Post-sunset Diffusion Artifact

In the usual graphic analysis of diurnal curves, after selection or computation of k, the diffusion correction is applied for each hour of the day and night so that the final rate of change graph indicates only the photosynthetic and respiratory metabolic rates. When no allowance is made for changing constants and where there is a change of reaeration rate due to wind variation, some artifacts are produced. One of these artifacts has been observed frequently, a post-sunset bulge. Where this irregularity is recognized it may be allowed for in metabolic computations. Field measurements of wind velocity with a hand anemometer are now a standard part of the diurnal procedure.

In many localities on the Texas coast particularly in summer there is a marked sea-breeze-landbreeze effect so that the prevailing southeast trades pulse with diurnal variation. The bay waters are much more vigorously mixed in the evening than in the early morning. There is a resulting diurnal change in the reaeration constant. Because many of the curves pass through saturation about sunset, the error is not great in most instances. However, if one uses one reaeration constant uniformly during a night, one introduces an artifact that looks like a burst of post-sunset photosynthesis (Fig. 5 and 6). This graphic artifact develops because one undercorrects for aeration early in the evening and overcorrects later. One may suspect this effect whenever the post-sunset oxygen curve is concave downward. To avoid the effect one may use a different k in the early evening from that used later at night using wind observations and Fig. 4 to estimate a suitable k.

Results

In the paragraphs that follow photosynthetic and respiratory data are presented for several situations and seasons with an interpretive emphasis on the special features discussed in each case as a natural experiment. P is gross production; R is total community respiration.

The various new refinements in analysis of these graphs have been applied to older data wherever used in this paper so that the values in Fig. 7 may not be exactly the same as previously published in some instances.

In presenting diurnal data from a 24 hour series, all items are arranged with noon in the middle of the graph even though the series began at any time of the day. The right side of the graph may be earlier in time than the left side. The time of start is indicated by a break in the line connecting the points. One should not compute a rate of change for the segment connecting the start to the end, as such a segment is not real. One may connect the points on the rate graph across such a gap in order to compute photosynthetic areas without affecting values appreciably.

Seasonal Cycles in the Laguna Madre, a Thin-grass System

With the help of many persons and as part of several related studies, diurnal curve measurements have now been made in the Laguna Madre over a period of 4 years including dry and wet years. The measurements in the first year were made in a slightly more inshore station inside Pita island than in later years when the curves were taken outside of Pita island. Data on photosynthesis, respiration, computed diffusion constants, salinity and temperature are reported in Fig. 7.

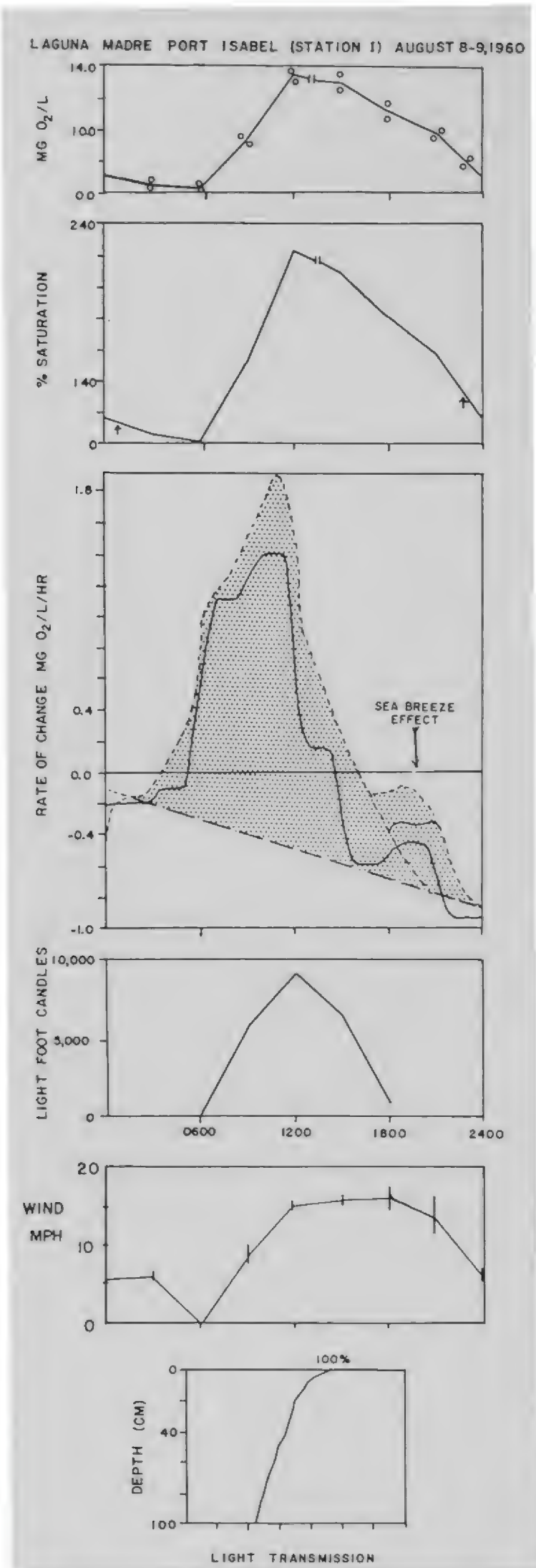

FIG. 5. Diurnal curve showing the post-sunset bulge artifact due to decreasing winds and aeration after dark frequently found in Texas due to seabreeze effects. Grass flats in the Lower Laguna Madre at Port Isabel, 1.4 m, salinity 36.7‰, wind velocities in mph.

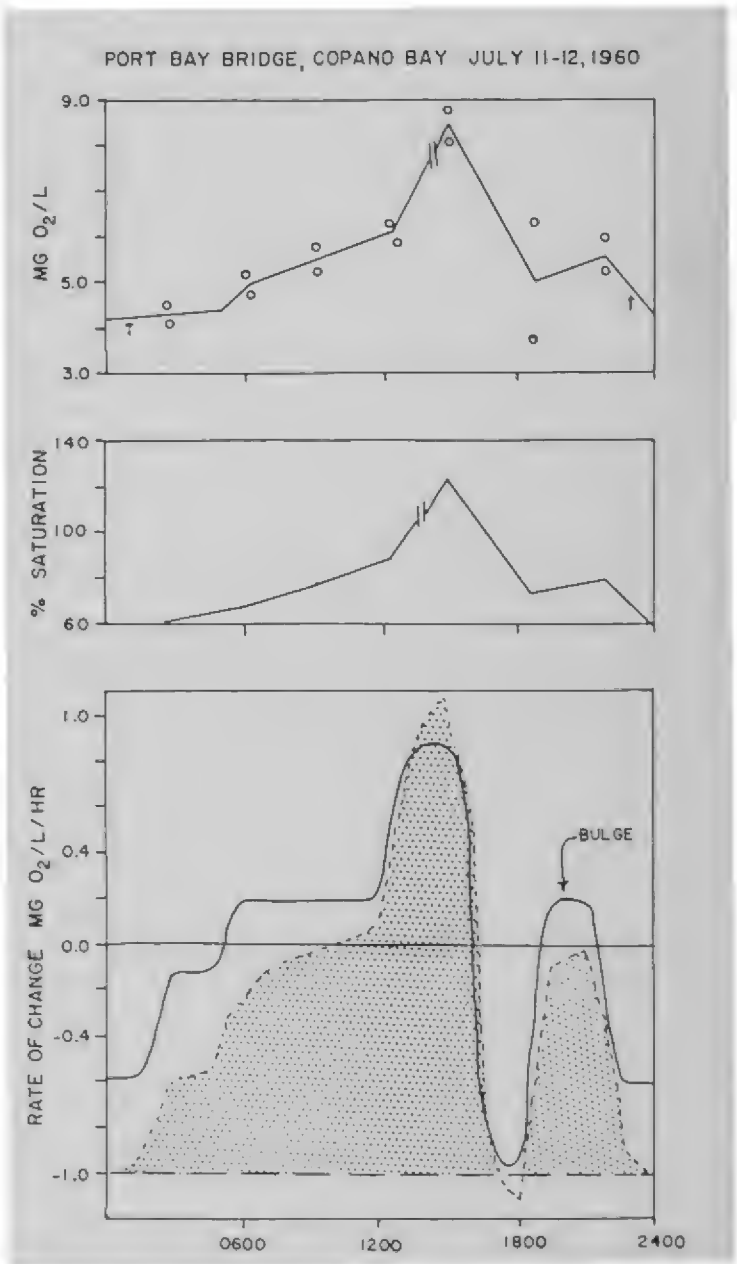

FIG. 6. Diurnal curve with post-sunset bulge artifact in Port bay, a low salinity arm of Copano Bay receiving Aransas River. Depth 0.92 m; salinity 13.6 ‰, July 11–12, 1960.

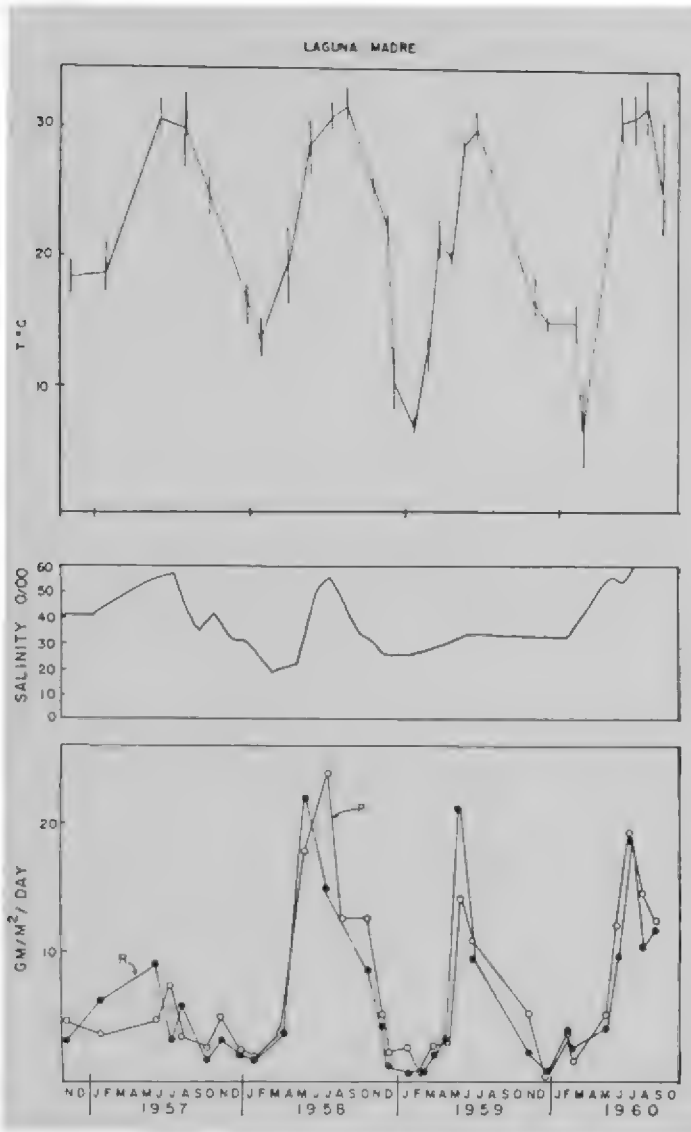

FIG. 7. Four year record of gross photosynthesis (P) and community respiration (R) in the Laguna Madre. Each point represents a diurnal curve on a particular day as indicated. Salinities and temperatures (daily ranges) are also plotted for the particular days of the 24 hr studies.

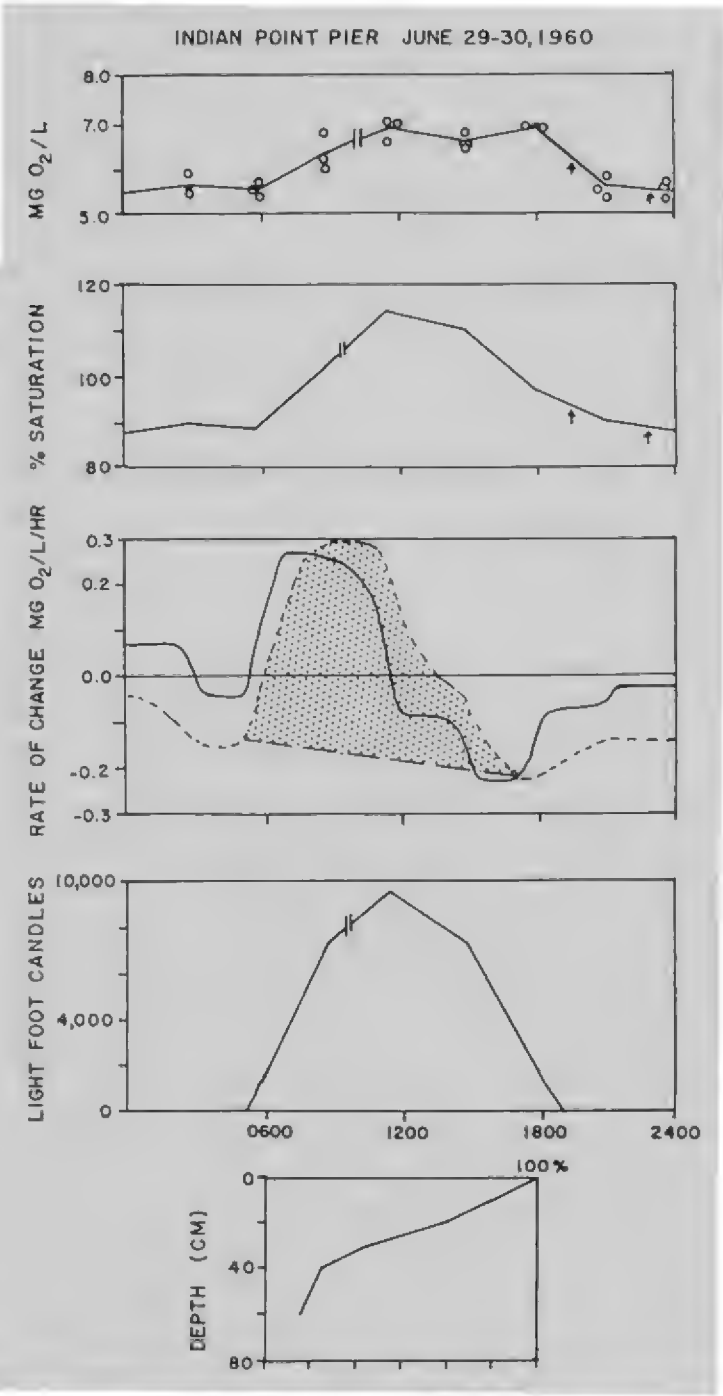

FIG. 8. Diurnal curve for Corpus Christi from Indian Point Pier, July 29–30, 1960. Salinity 34.6 ‰; water depth 3 m; temperature range 28 to 32° C; wind 7 to 14 mph. A typical graph for a deeper bay.

The upper Laguna Madre in the study area is carpeted with a firm bottom and fine grass in water about one meter in depth. In the dry years with the salinity above 40 ‰ this grass was almost exclusively composed of *Diplanthera wrightii,* but during the relatively wet year of 1959 considerable *Ruppia maritima* developed, diminishing again in 1960.

Only in summer 1960 were dense mats of dead grass observed accumulating. In general consumption and production were closely correlated. There was an immense difference between the winter and the summer (Fig. 7). Whereas 96,000 foot candle-hours were received on a representative summer day July 25, 1960, only 4500 foot candle-hours were received on a cloudy winter day Dec. 8, 1960, and 19,500 foot candle-hours on a clear day in winter, Dec. 28, 1961. The low winter photosynthetic productivities thus were correlated with winter cloudiness and short days. Unlike Florida at a similar

latitude, the cloudiness in Texas was maximal in winter. There was thus a tremendous annual pulse in the energy entering the biological system. The observed photosynthesis reflects this cloudiness. The close correspondence of respiration with photosynthesis without lag suggests that the life cycles of the organisms are sufficiently adjusted to provide almost simultaneous increase and decrease of consumer populations to maintain equivalence of P and R. The migration of mullet, shrimp, crabs and other consumers from the Laguna (Hellier, 1962) is a part of this system which diminishes winter metabolism as the photosynthesis drops. There is relatively little lag.

The temperature sequence parallels photosynthesis only in part. Productivities fall rapidly after July whereas temperature does not diminish appreciably until November. See plot of temperature by Hellier (1962). Although the decrease in salinity produced some differences in plant type, gross photosynthesis was little affected.

Metabolism in Corpus Christi Bay, a Planktonic System

A very different type of ecosystem, the deeper bay, is represented by Corpus Christi Bay, a large moderately turbid system 3 to 4 m deep, in which wind and waves provide a strong circulation. Salinity studies such as that by Hood (1953) indicate a generally counterclockwise circulation as might be expected for a body receiving freshwater river flow. The salinity varies markedly between wet and dry years with values ranging from 10 to 45 ‰. The bay metabolism is based on a plankton system. The shade of the relatively deep and turbid water prevents growth of extensive grass areas. Several industrial effluents enter along the margins. A typical diurnal curve is given in Fig. 8.

Data were collected on Corpus Christi Bay over a period of several years as indicated in Table 1. In general the oxygen amplitude was slight and production usually relatively small per volume (one or two mg/l/day). In the total water column, however, combined production and respiration approached values for other bays. The diurnal curve for Indian Point Pier, June 29–30, 1960, (Fig. 8) is representative.

Along the waterfront at Corpus Christi is a protected area behind a breakwater. In this inner area there was calm water with some stagnation and opportunity for fertilizations and pollutions from boat activity. In this "T head" area an instance of high metabolism is reported (Table 1).

Synoptic Comparison of Metabolism of the Texas Bays in Summer

During summer (June-August), 1960, an intensive effort was made to measure the metabolism of a number of the bays of Texas during the same summer season. The resulting values for gross photosynthesis and total respiration are plotted in Fig. 9. The grass and plankton types are represented as already described, but each bay has distinctive features.

The general high level of summer metabolism is again demonstrated as compared with values of 1 gm/m^2/day for the central oceans (Ryther, 1959). The back bays in drowned river valleys with values from 1 to 12 gm/m^2/day were somewhat less productive than some of the front bays along the beach barrier, not immediately part of the river valleys.

In general the back bays and those with river inflows receive more turbid drainages, more pollutions, more wind disturbances, more flushing, and more shocks of high and low salinity variation. These factors may be responsible for lower sustained photosynthesis values.

TABLE 1

Gross production, community respiration, and reaeration constants for Texas bays. Data for Redfish Bay and Laguna Madre are in Figures 7 and 21. An asterisk (*) indicates that data were not suitable for computing reaeration constant.

	Date	Depth m	Salinity ‰	Temperature °C	P gm/m²/ day	R gm/m²/ day	K gm/m²/ hr at 0%
NUECES BAY							
Outlaw Bait Stand	July 30–31, 1959	0.25	15	28–33	2.7	2.2	0.4
Outlaw Bait Stand	July 16–17, 1960	0.61	35	29–33	12.9	7.9	0.6
Near East end of causeway	July 16–17, 1960	0.3	35	29–34	5.6	0.9	*
OSO BAY							
Under Bridge	June 30–31, 1959	0.6	22	26–34	6.8	2.4	1.0
SAN ANTONIO BAY							
Hynes Bay	July 11–12, 1960	0.5	2	27–35	4.2	9.3	0.8
Hoppers Landing	July 11–12, 1960	0.4	6	28–34	2.7	5.7	0.6
Gonzalez Camp	July 11–12, 1960	0.5	8	27–35	4.3	6.2	0.7
MESQUITE BAY							
Red Algal Bottom	July 22–23, 1957	0.7	15	28–31	3.7	7.3	0.7
Shell Bottom	July 22–23, 1957	1.0	16	28–31	2.1	5.8	0.8
Cedar Bayou	July 22–23, 1957	1.5	25	28–31	2.4	2.0	2.2
ARANSAS BAY							
Hunt's Pier, Rockport	May 19–20, 1957	2	21	26–28	10.0	9.6	*
Rockport Basin	Aug. 5–6, 1957	1.5	34	31–32	6.1	11.5	1.1
Hunt's Pier, Rockport	Oct. 20, 1957	1.3	19	22–26	6.1	7.8	1.8
A & J Pier, Rockport	July 10, 1959	1.0	20	29–32	3.6	2.4	1.0
Hunt's Pier, Rockport	July 11, 1960	2.0	21	28–32	6.8	10.9	2.7
LOWER LAGUNA MADRE							
Port Isabel, Sta. 1	Aug. 8–9, 1960	1.4	37	28–30	26.3	13.8	0.7
Port Isabel, Sta. 2	Aug. 8–9, 1960	1.4	37	28–30	30.0	19.7	1.0
Port Isabel, Sta. 3	Aug. 8–9, 1960	0.9	37	28–30	22.6	6.7	1.3
Port Mansfield, Sta. 1	July 25–26, 1960	0.9	36	28–31	11.7	4.3	0.7
Port Mansfield, Sta. 2	July 25–26, 1960	1.4	41	29–31	17.3	19.7	0.6
Port Mansfield, Sta. 3	July 25–26, 1960	1.4	39	29–31	22.5	21.4	1.4
BAFFIN BAY							
County Pier, Loyola	Feb. 4, 1957	1.0	79	23–25	16.6	9.6	2.3
County Pier, Loyola	June 12, 1957	1.0	45	29–32	4.2	12.9	1.0
County Pier, Loyola	July 26–27, 1957	0.9	57	28–33	7.8	13.8	0.9
County Pier, Loyola	Aug. 15–16, 1957	0.9	65	29–32	6.9	8.8	0.9
County Pier, Loyola	Nov. 14–15, 1957	1.7	78	15–20	7.1	4.0	1.0
County Pier, Loyola	Dec. 22–23, 1957	0.8	63	19–21	4.0	5.1	1.3
County Pier, Loyola	Sept. 3–4, 1958	1.0	42	28–31	2.4	3.4	0.8
County Pier, Loyola	June 18–19, 1959	1.3	30	28–31	12.2	25.3	1.3
County Pier, Loyola	Sept. 7–8, 1959	0.9	41	27–30	5.9	8.3	0.7
County Pier, Loyola	Dec. 1–2, 1959	1.0	49	14–17	1.7	1.8	1.5
County Pier, Loyola	Jan. 8–9, 1960	1.1	49	12–15	4.7	2.4	1.1
County Pier, Loyola	April 11, 1960	1.1	51	22–25	9.0	19.8	2.4
County Pier, Loyola	June 21, 1960	0.9	61	28–32	3.5	9.7	0.8
County Pier, Loyola	July 12, 1960	1.4	59	28–32	6.4	13.2	*
Off Riviera Beach	June 28, 1960	1.6	53	28–30	19.2	18.4	2.2
Middle Bay	July 5–6, 1960	0.8	51	28–31	4.3	8.3	0.4
Penescal Point	July 7–8, 1960	1.0	47	28–31	3.5	7.3	0.5
Alazan Bay	July 14, 1960	1.3	59	28–33	12.5	13.5	0.8
SEWAGE LAGOONS, TEXAS HEALTH DEPARTMENT DATA							
San Marcos	July 12, 1948	0.8	fresh	27–30	17	14	0.6
San Marcos	July 14, 1948	0.8	fresh	27–30	46	25	1.7
San Marcos	July 20, 1948	0.8	fresh	27–30	21	25	1.1
San Marcos	Aug. 5, 1948	0.8	fresh	27–30	32	27	0.5
SABINE BAY							
Port Arthur	June 27, 1960	2.0	15	27–31	8.8	11.3	2.0
CORPUS CHRISTI BAY							
Ingleside, Moores Pier	June 21–22, 1957	1.4	23	28–30	5.3	7.9	0.7
Indian Point Pier	June 26–27, 1959	3.0	28	28–29	6.8	9.4	*
Indian Point Pier, tropical storm	June 23–24, 1960	3.0	30	26–29	7.8	25	*
Indian Point Pier	June 29–30, 1960	3.0	35	28–32	9.6	12.3	3.0
T Head	June 15–16, 1960	3.1	33	27–30	20.4	21.6	*

TABLE 1—Continued

Gross production, community respiration, and reaeration constants for Texas bays. Data for Redfish Bay and Laguna Madre are in Figures 7 and 21. An asterisk (*) indicates that data were not suitable for computing reaeration constant.

	Date	Depth m	Salinity ‰	Temperature °C	P gm/m²/day	R gm/m²/day	K gm/m²/hr at 0‰
North Beach, pier, tropical storm	June 23–24, 1960	2.4	31	26–29	3.8	18.4	*
North Beach, pier	June 29–30, 1960	2.4	34	27–29	13.4	13.7	4.6
Oso Pier	June 30–31, 1960	3.0	29	28–30	7.5	10.8	*
Oso Pier	July 5–6, 1960	3.7	34	28–32	26.6	18.6	*
COPANO BAY							
Bayside	Oct. 20–21, 1957	2.0	18	22–25	1.6	1.7	*
Route 35 bridge	May 19–20, 1957	1.0	13	26–29	5.0	7.2	3.8
Port Bay bridge	May 19–20, 1957	1.0	30	26–31	3.6	4.3	0.4
Bayside, pier	Aug. 8–9, 1957	1.5	12	30–32	5.0	14.7	3.4
Bayside, pier	July 11–12, 1960	1.5	6	28–31	10.5	24.1	2.7
Port Bay bridge	July 11–12, 1960	0.9	14	27–32	14.0	22.0	0.9
MATAGORDA BAY							
Lavaca Bay Bridge	June 17–18, 1957	1.5	5	29–30	1.0	7.8	1
Lavaca Bay Bridge	July 15–16, 1960	1.7	1	29–32	10.4	4.0	2
Tres Palacious, pier	June 17–18, 1957	1.0	4	29–31	3.8	5.8	0.8
Tres Palacious, pier	July 14–15, 1960	1.0	3	29–32	12.5	0.5	1
Caranchua Bay Bridge	July 4–15, 1960	0.9	1	28–34	6.0	4.4	0.6
SLOUGHS AND BOAT HARBORS, Port Aransas							
Shell Shop Pond, Fig. 2, No. 2	July 1–2, 1957	1.0	26	28–30	5.3	11.7	1.3
Shell Shop Pond	July 21–22, 1960	0.4	39	29–37	14.7	13.7	0.3
Shell Shop Pond	July 27–28, 1960	0.4	39	29–31	5.8	10.0	*
Shell Shop Pond	Aug. 3–4, 1960	0.4	39	29–35	12.0	5.5	0.3
Shell Shop Pond	Aug. 10–11, 1960	0.4	38	30–36	11.6	9.1	*
Shell Shop Pond	Aug. 16–17, 1960	0.4	36	30–34	10.6	6.1	0.4
Shell Shop Pond, after hexadecanol added	Aug. 18–19, 1960	0.4	36	30–35	11.0	7.4	0.3
Port Aransas Beach pool near jetty, Fig. 2, No.1	July 1–2, 1957	0.15	25	27–32	1.5	3.7	0.3
Pond, Fig. 2, No. 3	July 5–6, 1960	0.3	30	27–36	3.0	4.3	*
Pond, Fig. 2, No. 3, after fertilization	July 18–19, 1960	0.3	35	27–36	12.0	12.7	0.3
Pond, Fig. 2, No. 3	July 21–22, 1960	0.3	35	28–37	11.4	9.1	0.2
Pond, Fig. 2, No. 3	July 27–28, 1960	0.3	34	29–36	10.0	10.2	0.4
Pond, Fig. 2, No. 3	Aug. 3–4, 1960	0.3	30	28–36	7.1	6.5	0.2
Pond, Fig. 2, No. 3	Aug. 10–11, 1960	0.3	45	29–36	8.0	5.8	0.3
Pond, Fig. 2, No. 3	Aug. 16–17, 1960	0.2	34	30–36	3.2	1.7	0.5
Pond, Fig. 2, No. 3, hexadecanol added	Aug. 18–19, 1960	0.2	34	30–35	4.6	5.7	0.2
Ferry Road algal mat, Fig. 2, No. 4	July 5–6, 1960	0.13	35	27–37	2.9	2.2	0.16
Ferry Road algal mat, trace metals added	July 18–19, 1960	0.13	40	27–38	5.4	6.6	0.26
Ferry Road algal mat	July 21–22, 1960	0.13	40	27–39	6.6	6.6	0.27
Ferry Road algal mat, Fig. 2, No. 4	July 27–28, 1960	0.05	....	26–40	....	....	....
City Launching Basin, (by G. Kone) Fig. 2, No. 5. Sta. a	July 25–26, 1959	2	33	30–32	4.3	4.4	0.6
City Launching Basin, (by G. Kone), Sta. b	July 25–26, 1959	2	34	29–31	4.2	4.7	0.8
City Launching Basin, (by G. Kone), Sta. c	July 25–26, 1959	2	34	29–31	5.3	9.4	2.9
City Launching Basin	Aug. 10–11, 1959	2	34	30–32	9.8	9.6	1.6
City Launching Basin	July 5–6, 1960	2	32	29–32	6.8	9.7	1.2
City Launching Basin	July 18–19, 1960	2	38	30–32	18.0	9.7	1.8
City Launching Basin	July 21–22, 1960	2	39	29–33	3.8	1.4	1.3
City Launching Basin	July 27–28, 1960	2	39	30–33	....	....	....
City Launching Basin	Aug. 3–4, 1960	2	32	30–33	17.7	6.0	1.0

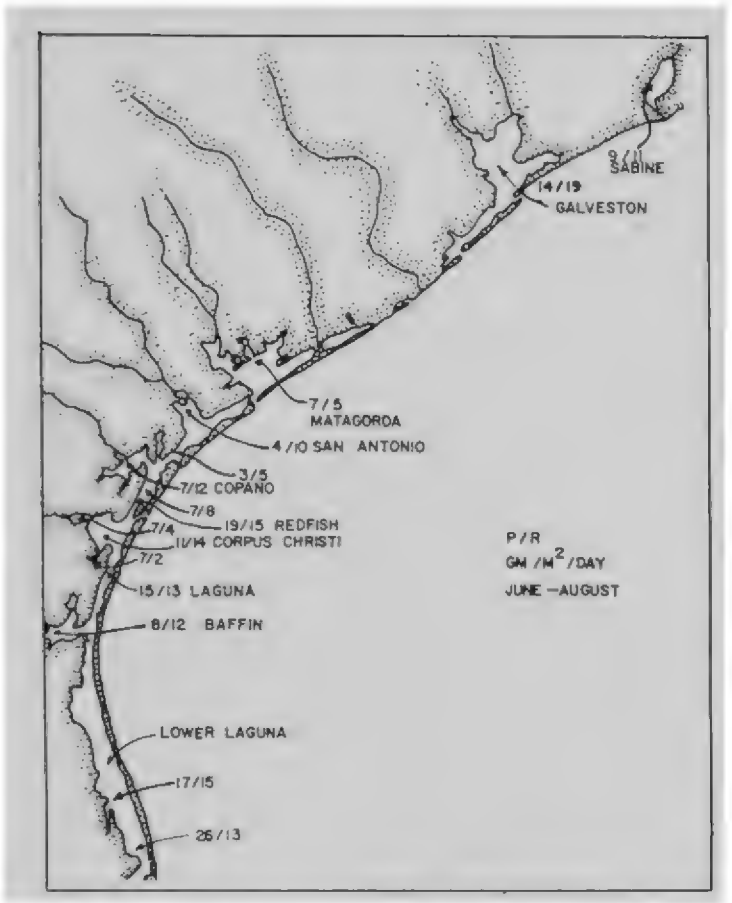

FIG. 9. Synoptic map of gross photosynthesis (P) and twenty-four-hour respiration (R) in Texas bays in June, July, and August, 1960. Each value is given in gm oxygen/m^2/day. The upper value is gross photosynthesis; the lower value is total community respiration. Galveston values in 1961, July 15–19: Eagle Point, West Bay, and Lower-center of Trinity bay (field assistant, N. Vick). Each number is a mean of three.

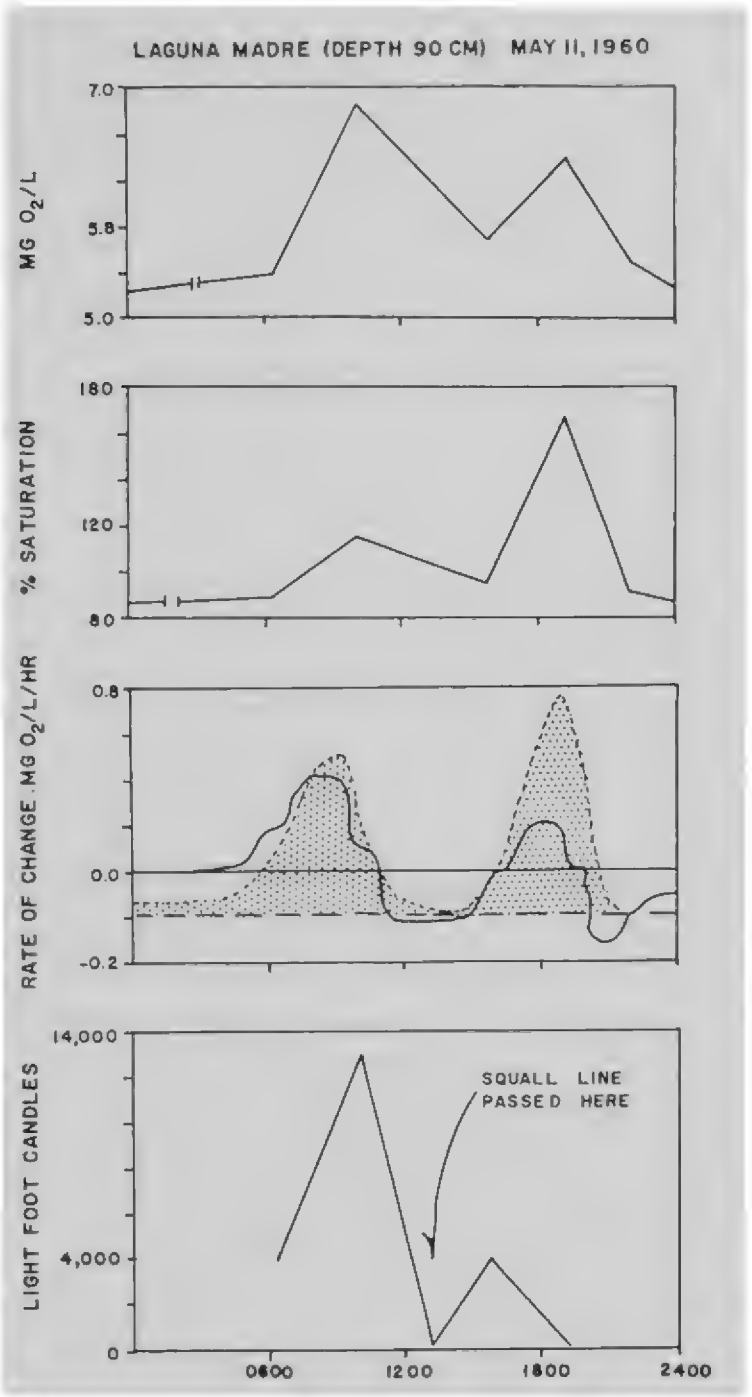

FIG. 10. Diurnal curve in the Laguna Madre, May 11, 1959, showing the passage of a cold frontal squall line with a zone of heavy cloudiness in the middle of the day. Salinity 49 ‰, depth 0.9, temperature range 24 to 24°C, wind light except 60 mph during squall passage.

Whereas the front bays (Laguna Madre and Redfish Bay) are shallow and often grassy, the back bays tend to be deeper with insufficient light reaching the bottom for fully developed production. Where they can develop, the benthic communities are generally more fertile than the plankton communities as illustrated by data in Table 1.

High gross productivity is correlated with the establishment of a stable community with its self-contained nutrient cycle. Thus the very high salinity conditions of 40 to 70 ‰ in Baffin Bay and Laguna Madre although unfavorable to particular species are apparently not detrimental to overall production and respiration since highest values are obtained in these regimes. Where evaporating conditions are developing, nutrients are conserved, concentrated, and biota may be stabilized.

The general patterns of metabolism with time and space were outlined in Figs. 1–9. Next consider some special cases.

Metabolism During Passage of a Densely-cloudy Cold Front

On May 11, 1959, a diurnal curve was taken in the Laguna Madre in which a norther passed in the middle of the day. The data are presented in Fig. 10. As indicated in the foot candle graph the frontal cloudiness was sufficient to reduce the light available to photosynthesis to 5% of that which preceded and followed the passage of the sharp frontal squall area. An interruption of photosynthesis was produced by the interruption of light. Similar instantaneous changes in photosynthetic rate have been observed with changes in cloud cover in many graphs.

Metabolism During Days of Minimum Temperature in Winter

In the seasonal record of metabolism in Fig. 7, the winter days reported are unrepresentatively high since the data were generally collected between cold spells on relatively sunny days and at times of higher temperature. In the series for Laguna Madre, February 24, 1960, however, a special effort was made to obtain data during one of the cold, cloudy periods accompanied by the strong north winds typical of winter northers in Texas.

Examination of the oxygen graphs in Fig. 11 shows the effect of temperature change in modyfying the oxygen content of the bay waters. With thirty mile per hour winds

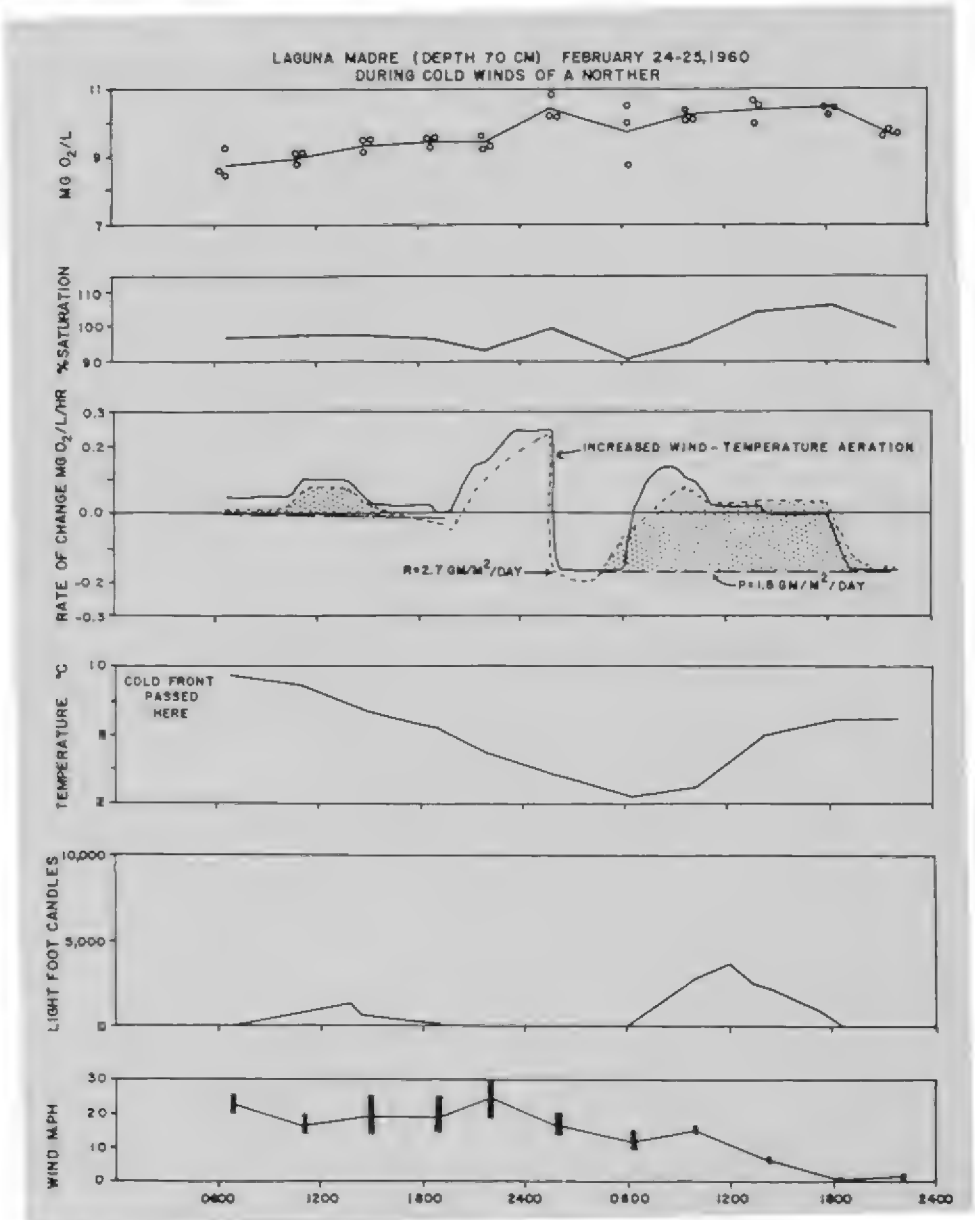

Fig. 11. Diurnal oxygen curves for Laguna Madre, February 24 and 25, 1960, during the weather regime associated with passage of a cold norther and later return to more normal temperatures. Salinity 31 ‰, depth 0.70 m.

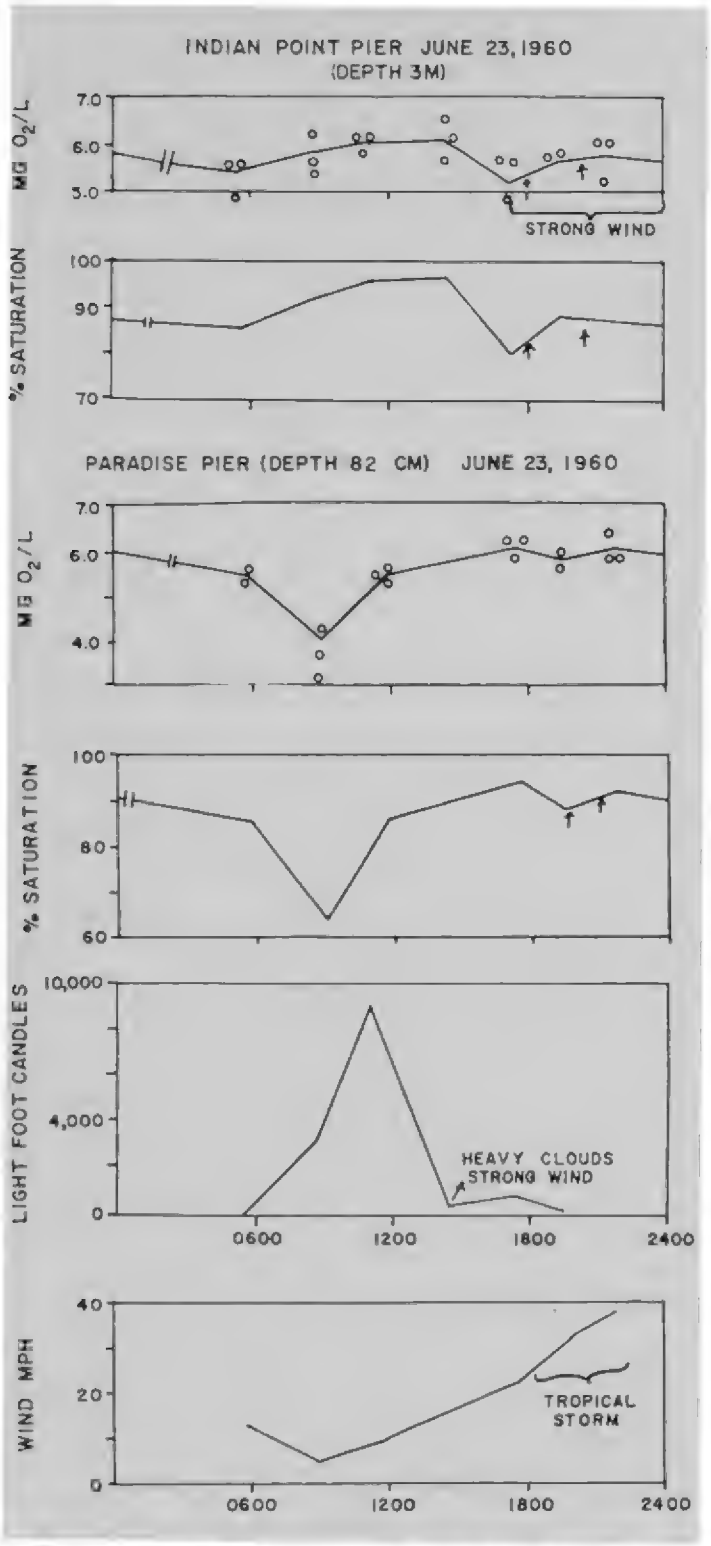

FIG. 12. Diurnal curves at two stations in Corpus Christi bay June 23, 1960, as a tropical storm approached, accelerating winds, and lowering heavy clouds. This is an example of the effect of an increasing reaeration rate during the course of the day.

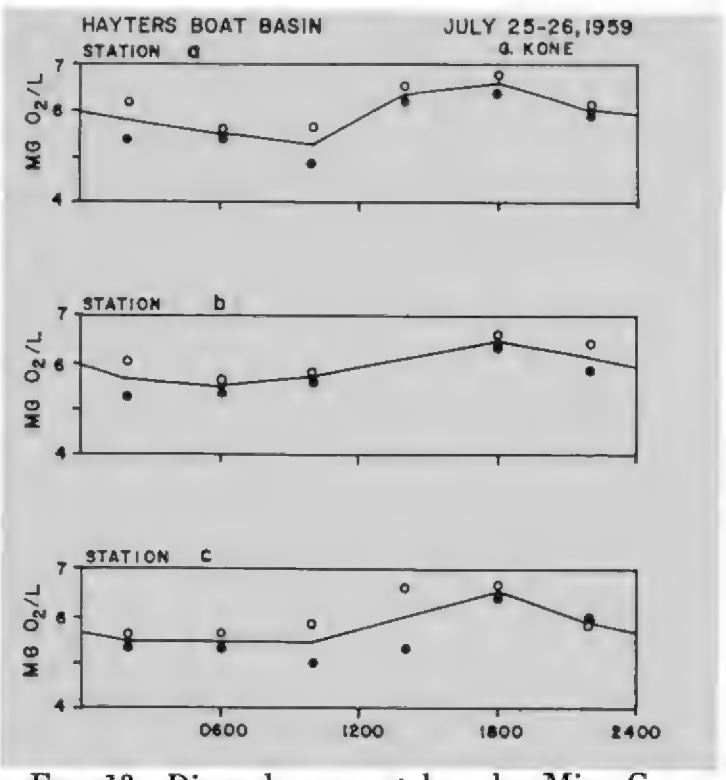

FIG. 13. Diurnal curves taken by Miss Gertrude Kone in a new small boat harbor, Port Aransas, Texas, July 25–26, 1959. Clear circles are surface samples; solid circles are bottom samples. See Fig. 2 for map showing stations a, b, and c.

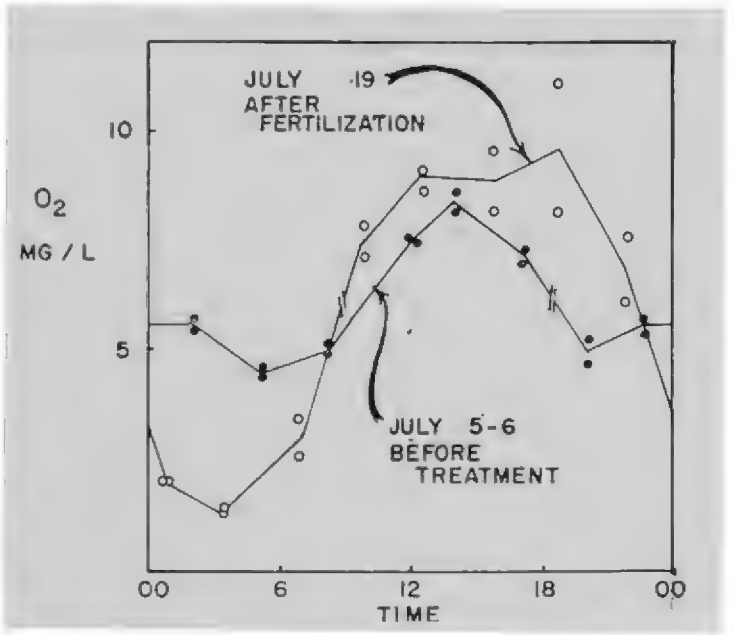

FIG. 14. Diurnal curves for the Oppenheimer House Slough before and after fertilization with nitrogen-phosphorus fertilizer. See Fig. 2, pond No. 3.

blowing polar air over bays 0.5 to 1 m deep there was a rapid fall of temperature of the water, corresponding increase in saturation capacity of the water, and influx of oxygen by diffusion. Under conditions of rapid diffusion due to wind agitation, conditions are not optimal for application of the diurnal curve methods. Nevertheless when the diffusion correction was applied in the usual manner and the oxygen that had diffused in was removed from the rate of change curve (Fig. 4), a definite though small photosynthesis was found. Even though temperature changes are large and rapid in the bays in winter, the metabolism and photosynthesis of the communitties does continue. Some acclimation is suggested by the greater respiration the second day.

During the same period a 24 hour dark-light experiment was run in triplicate with bot-

tles at surface and bottom. On an area basis plankton metabolism estimated from bottles was 0.28 gm/m²/day respiration and 0.49 gm/m²/day gross photosynthesis. As in previous comparisons of bottle and freewater data, higher values in the freewater indicate importance of bottom components (Odum and Hoskin, 1958).

Comparison of Metabolism on Successive Clear Days and Cloudy Days

In the *Thalassia-Diplanthera* grass of Redfish bay diurnal curves were taken for a pair of successive clear and coludy days in winter, January 31-February 1, 1957, and for a pair of successive clear and cloudy days in summer, August 10–11 and August 13–14, 1960. The data in Table 1 indicate a very large range in photosynthesis from day to day correlated with cloudiness. In winter the sunny day was 50% more productive: (clear day, P = 6.3 gm/m²/day; overcast day, P = 3.9 gm/m²/day); in the summer example 4 times more productive; (clear day, 10,000 foot candles at noon, P = 38.5, R = 33.0 gm/m²/day; cloudy day, 3,000 foot candles at noon, P = 8.5, R = 7.9 gm/m²/day). Apparently the respiration was a function of the photosynthesis since it diminished on the cloudy day. Beyers (1962) found a close correspondence between community respiration and community photosynthesis in microcosms from day to day, P depending on the preceding R and vice versa.

Metabolism During Approach of a Tropical Storm

On June 23, 1960 a diurnal curve was obtained at two stations in Corpus Christi Bay as a tropical storm moved in. Data are presented in Fig. 12 and diurnal computation made on the mean curve. The winds increased from early morning at 5 mph to 40 mph by sunset occompanied by lowering ceilings and heavy rain. Reaeration was maximal by evening with waters swirling around the bay at a great velocity in water about 3 m deep. By evening the changing reaeration constant was 2 to 3. In spite of the tremendous reaeration rate, the oxygen remained in equilibrium below saturation presumably due to increasing respiration. The computed respiration rate necessary to balance reaeration was higher than usual for Corpus Christi Bay as might be consistent with high temperature, extensive agitation, and resuspension of bay bottom materials under maximum winds. The photosynthesis was measurable in the morning while the light intensity was appreciable before the onset of heavy afternoon clouds. The analysis of this curve is an example of use of the diurnal methods in a complex situation. Complex analysis cannot yet be turned over completely to routine assay.

Metabolism in a Small Boat Harbor

In spring, 1959, a small boat harbor was dredged into the land of the bar island at Port Aransas producing a stagnant arm of the sea about 4 m deep, 30 m wide, and 300 m long (Fig. 2). Shortly after its formation in summer diurnal curves were run for 3 stations (Fig. 2: a, b and c) in this body by Miss Gertrude Kone as part of course requirement of General Marine Science with the results in Fig. 13. Data from the deeper of two sampling levels indicated a greater respiration than at the surface level, although stratification was not sharp. Computation of production was made with the mean of top and bottom samples.

After a year of heavy use by small boats, curves were again analyzed for the summer of 1960 with the results in Table 1. The use by the boats, fuel leakages, and other localized pollutions had apparently no great effect at that time. In spite of the considerable metabolism and sheltered nature of the basin, anaerobic conditions did not develop. There was considerable range in metabolism from day to day (1.4–18 gm/m²/day).

Metabolism of Sloughs

On the margins of the bays are small hollows, depressions, and pools at intertidal level containing 0.1 to 1 m of water. Some of these are connected with the main water body; others are isolated from normal water exchange. A series of measurements of metabolism was made in these sloughs. These bodies generally lack the strong circulation of the wind driven motion of the broad days of similar depth, but some have special localized sources of nutrients from pollutions, land drainage, or other cause. Diurnal curves were run on some of these sloughs as reported in Fig. 2, 14–16, and Table 1.

Whereas the daily range of oxygen was maximal in these bodies because all of the metabolism was compressed into a very thin layer, with the exception of the shell shop pond, the total metabolism per area (3–9 gm/m²/day) was not as great as in some of the larger bays that were better mixed and less disturbed such as Redfish Bay and Laguna Madre. All intertidal waters tended to be subjected to catastrophic drying during extremely low sets of the Gulf when water drained out of the bays for several days. Turbid flooding occurried at high tides, and fresh water flooded in during heavy rains.

During the period the shell shop pond was receiving fish offal and domestic pollution. Photosynthesis and respiration rates of that slough were greater than in the other littoral waters measured (5–15 gm/m²/day, Table 1).

Fertilization in Sloughs

In Fig. 14 are graphs for Oppenheimer House Pond, a small slough in which 50 pounds of nitrogen and phosphorus fertilizer powders were added July 18, 1960. As in other fertilization work in fish ponds, there was an immediate stimulation of photosynthesis (Table 1). Apparently the concentration of trace nutrients being maintained by the internal P-R cycle in the slough was less than the new concentrations which developed when the fertilizer was added. Subsequent measurements indicated a reurn to prefertilization values by the end of August a month later (Table 1). Respiration values followed photosynthesis values.

Metabolism in a Water Film System

One of the important ecosystems of the south Texas bay margins is the blue-green algal mat growing in films of water about 10 cm in depth. Diurnal curves in such systems as in the example in Fig. 15 provide some insight as to the kind of environment and productivity.

In spite of the extreme shallowness of the water, the range of oxygen was tremendous from anaerobic conditions to 240 per cent supersaturations in the course of the day. Contrary to expectations based on the theory that shallow waters are well aerated, the aeration is less effective in moderating the metabolism in the film community than in deeper systems. The action of metabolism tends to be concentrated in such

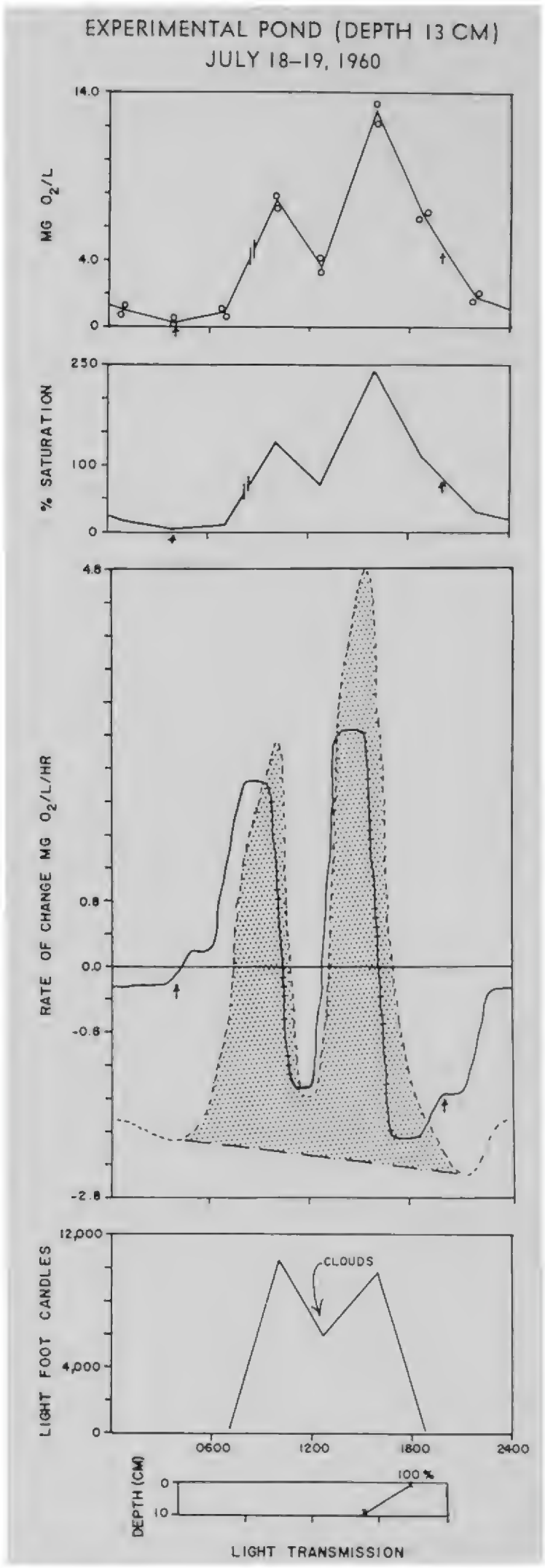

FIG. 15. Diurnal curve in a very shallow slough with 13 cm water over a benthic algal film community, along Ferry road, Port Aransas, July 18–19, 1960, salinity 39.6 ‰, wind 3–10 mph, uniform during period. See Fig. 2, No. 4.

a thin layer that diurnal changes are very large. The reaeration constant, on the other hand, on an area basis diminishes with depth (Fig. 3). In the example in Fig. 15, K is 0.25 gm/m²/hr/100%, and areation does not keep up with the wild swings of the concentrations in the film. For example just before noon, clouds diminished the light intensity as recorded in a drop from 10,000 to 6,000 foot candles. As instantaneous and marked drop in oxygen content occurred (Fig. 15).

It may be postulated that the reason for the dominance of the blue green algal mats in waters at 10 cm and not at greater depths is the anaerobic nighttime period in the film systems. Apparently the shallowest systems in the Texas bays are the only natural communities which regularly go anaerobic at night. The blue-greens survive.

The temperatures may also have a role in causing unusual biota. The diurnal range of temperature from 27 to 39°C in the very shallow waters and the wide fluctuation of oxygen contents tends to eliminate most consumer species thus favoring a net deposit of organic matter. The possible role of the algal mats in organic sedimentation has been already discussed (Fisk, 1959).

Hexadecanol Experiment in a Slough

Twelve pounds of hexadecanol were broadcast by hand on August 17, 1960, on water and marginal muds of each of two slough ponds (Fig. 2: Oppenheimer House Pond (No. 3) and Shell Shop Pond (No. 2) after diurnal curves had been made previously. Surface water ripples were visibly damped as the material was cast on the water in flakes, but by the end of the 24 hour period there was no sign of the hexadecanol over the water and the ripples were back to normal. Metabolic values were not markedly changed although there was possibly some increase in respiration over photosynthesis (Fig. 2 and Table 1). Harris and Meinke (1960) also reported an increase of bacterial action in sediments of fresh waters receiving hexadecanol due to metabolism of the solid alcohol material by the bacteria.

Metabolic Rates of Sewage Ponds

During World War II the Texas State Health Department made some studies of oxygen in experimental sewage lagoons. Some of these data were made available for the purpose of computing the total production and respiration. The data were derived from an unpublished report prepared by V. M. Ehlers, T. W. Ray, and E. C. Nelson in 1949.

The pond on the average was 0.75 m in depth, 41 m long, and 2.4 m wide. Supplementary lights were provided at one end. Some difference in oxygen values were found with about 1–4 ppm more oxygen in the lighted end. In recomputing the graphs for purpose of comparison with the natural bays, the data for the two ends of the long lagoon were averaged as presented in one series in Fig. 16. As included in Table 1 production ranged from 14 to 46 gm/m²/day with respiration in a similar range. P exceeded R in 3 of the diurnal curves but R was in excess in the fourth.

Respiration Excess in Back Bays

The back bays extending away from the beach line and receiving rivers developed respiration in excess of photosynthesis (Table 4; Fig. 1, 6, 17 and 18) suggesting a consumption of organic matter from an imported or previously stored source. R was greater

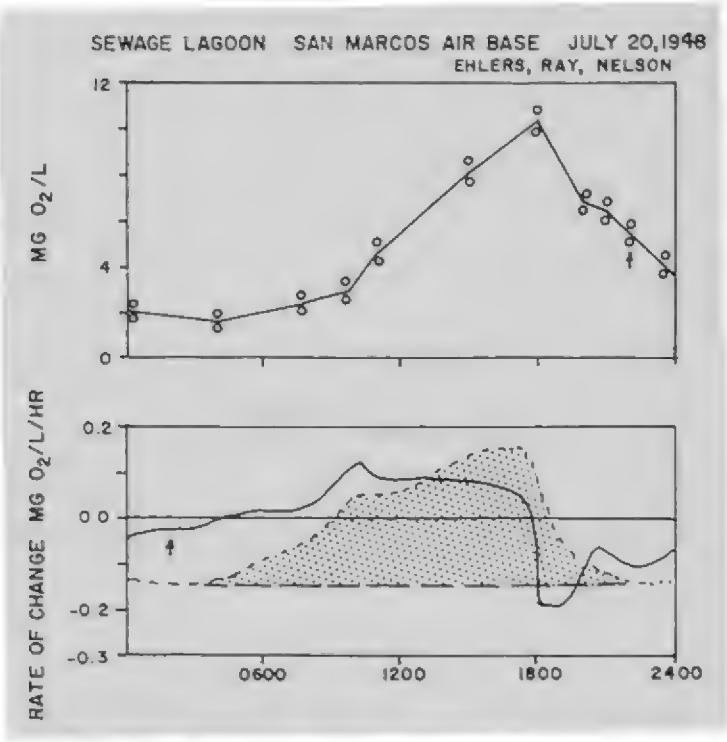

FIG. 16. Diurnal oxygen curve in a freshwater sewage lagoon, San Marcos, Texas, July 20, 1938. Data from Ehlers, Ray and Nelson. Depth 0.75 m: P, 21 gm/m²/day; R, 25 gm/m²/day. K = 1.05 gm/m²/100% deficit.

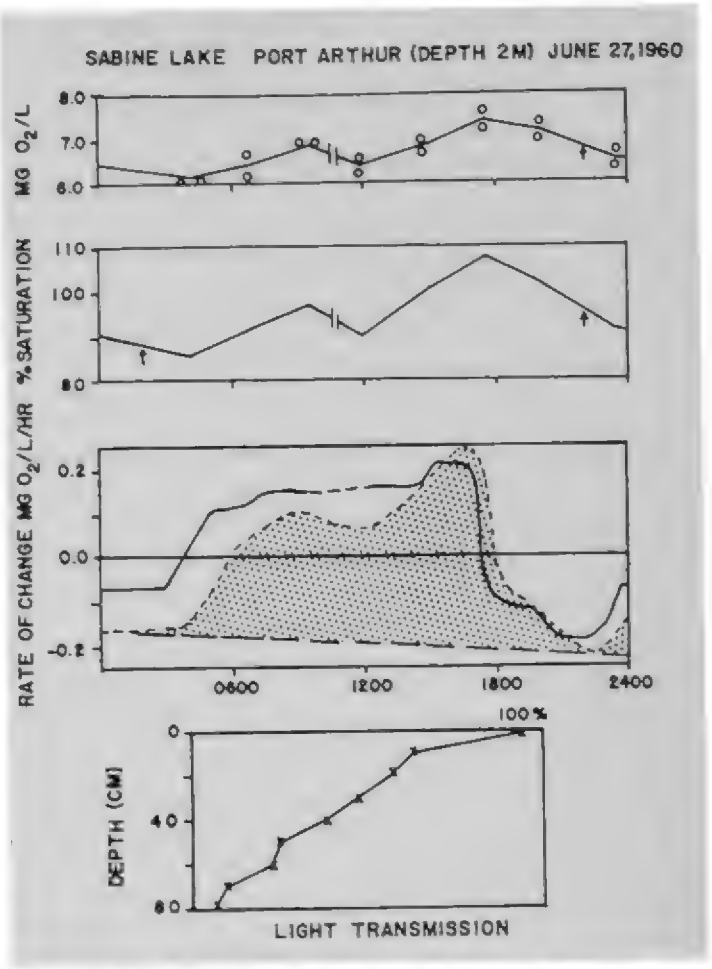

FIG. 17. Diurnal curve for Sabine Lake, Port Arthur, Texas, June 27, 1960. Salinity 15.4‰; depth 2 m.

than P at times of high turbidity both in low salinity conditions and in very high salinity conditions. Note frequent low P/R ratios for Baffin, Sabine, Lavaca, Corpus Christi, Copano and San Antonio Bays (Table 1). Baffin Bay is in a very arid area and was observed with an excess of respiration over photosynthesis for extended periods. The bay was continuously turbid suggesting a runoff of organic matter after cloudbursts over the arid lands of the surrounding King Ranch, little-covered with vegetation. Whereas the rains coming in floods were not frequent enough to equal evaporation, runoff was apparently adequate to supply the bay with enough particulate or other organic matter to maintain consumption in excess of photosynthesis.

Upper areas of San Antonio Bay at low salinity were observed with low P/R ratios near the bay delta of the Guadalupe River on two occasions also (Table 1). The Louisiana Bayou curves cited in a later paragraph are similar.

METABOLISM AFTER FLOODS

In 1960 a major flood developed in the Port Lavaca area with 15 inches rain causing the salinity of the arms of the Matagorda bay to fall to oligohaline amounts (less than 1 ‰). A diurnal curve measured in the headwater area during the flood runoff is presented in Fig. 19. Photosynthesis exceeded respiration. It is rather remarkable that photosynthesis was relatively high immediately after so sudden an upset. Apparently there are not always excesses in respiration in the runoffs. The quick recovery of the headwater producers was further established by Siler and Odum in an experimental pond microcosm with oysters and low salinity waters in which flooding rain waters were introduced. Photosynthesis returned to normal in several days.

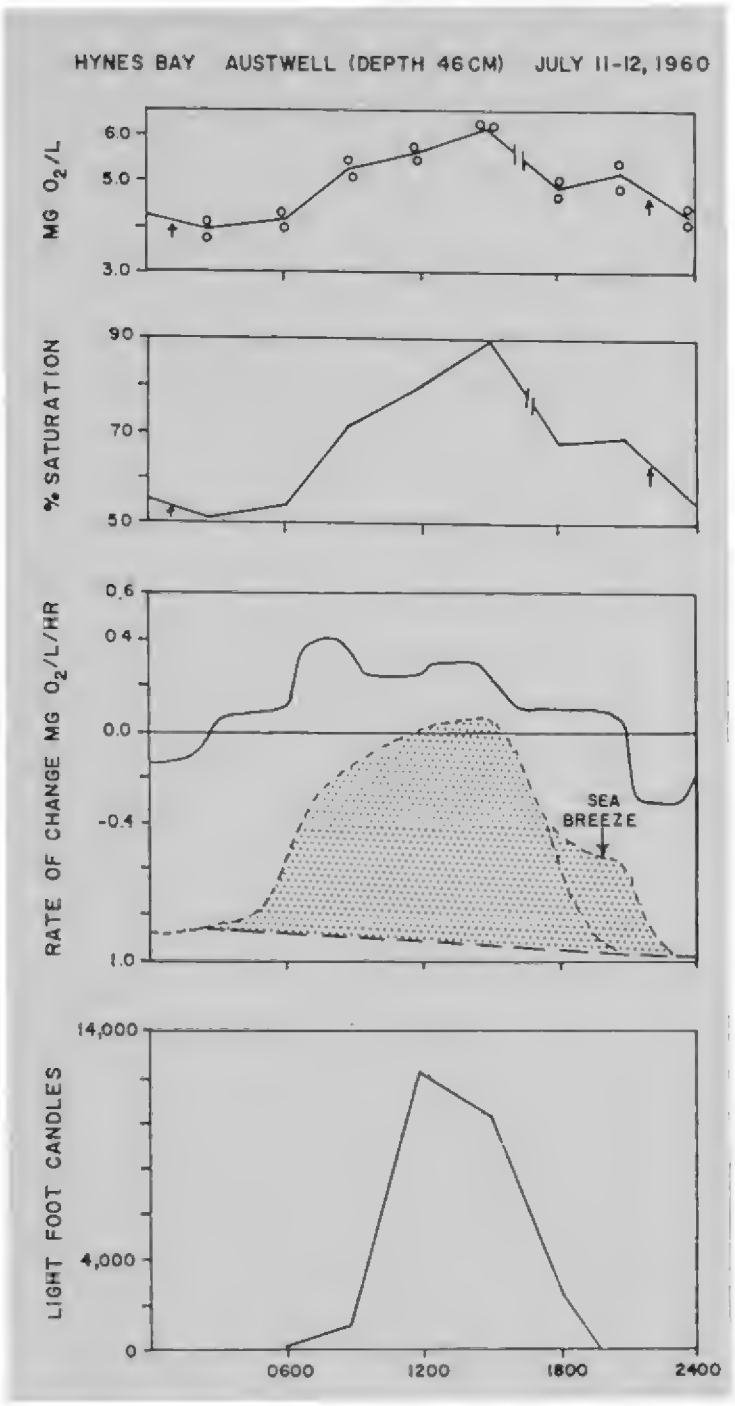

FIG. 18. Diurnal curve for Hynes Bay in San Antonio Bay, Texas, July 11–12, 1960. Salinity 1.8 ‰; depth 0.46 m; wind 12 to 15 mph in afternoon, 0 to 5 mph later at night.

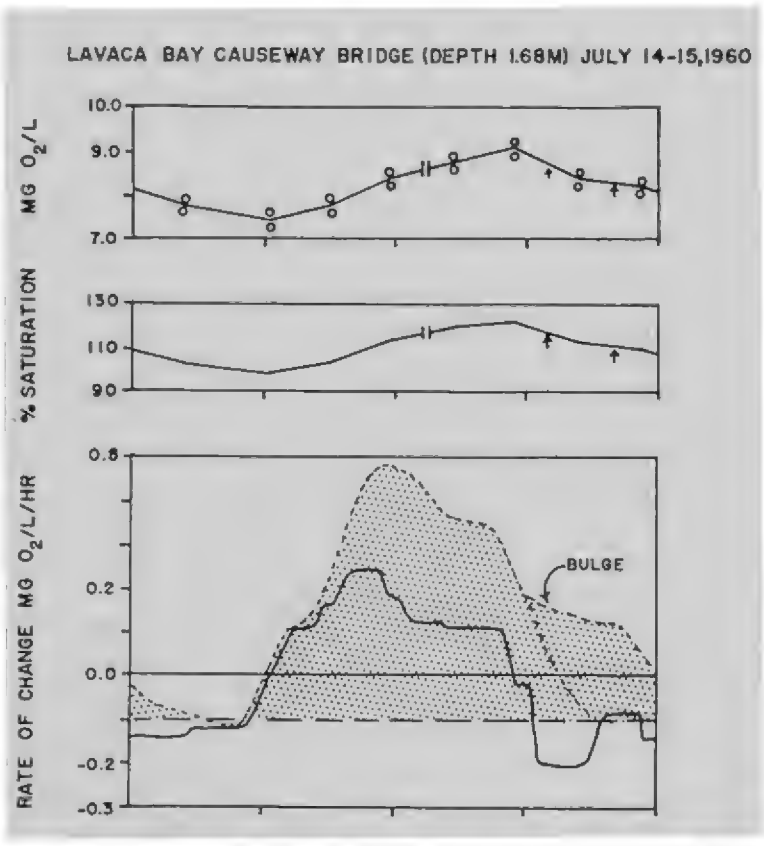

FIG. 19. Diurnal curve from causeway bridge in Lavaca Bay showing metabolism after a flood, July 14–15, 1960. Salinity 1.1 ‰, depth 1.7 m; wind 12–14 mph in the afternoon diminishing to calm in the morning.

METABOLISM AFTER DREDGING IN REDFISH BAY (Turtle Grass)

Another kind of inflow of turbid matter containing organic substrates occurred as a result of dredging of an intra-coastal channel near Redfish bay. Two diurnal curves were made during the dredging while the clouds of turbid water were drifting over the stations. The first off Bishop Pier in 2 m water March 10–11, 1959, at salinity 18.2 ‰ produced values: P, 3.0 gm/m²/day and R, 12.4 gm/m²/day. The second curve near Ransom island in 1 m depth Aug. 5–6, 1959, over grass flats at salinity 29.8 ‰ yielded values, P, 13.6 gm/m²/day and R, 17.3 gm/m²/day. Thus in both cases respiration much exceeded photosynthesis during the dredgings.

After the dredging a light layer of silt was deposited over the turtle grass flats as described elsewhere (Hellier and Kornicker, 1962). It is apparent that respiration exceeded photosynthesis, possibly due to the consumption of organic matter added with the spoil sediments.

The photosynthesis was not much diminished during or after dredging as compared

with data from a previous year. The additional respiration due to extra organic matter did not apparently interfere with normal production. High production and dense grass found after dredging may have resulted from release of nutrients.

Metabolism in an Enclosure over Turtle Grass

In Redfish Bay in June 1958 a fiber glass enclosure was constructed with 3 fiber glass sheets each 3 m long arranged in a triangle so as to make a tank. This enclosure was set over the turtle grass beds in 0.5 m depth at station 2 in Redfish bay. On June 10 a diurnal curve was run on the inside and on the outside. The mean curves are similar as indicated in Fig. 20. Metabolism was similar outside the enclosure (P, 6.4 gm/m²/day; R, 11.8

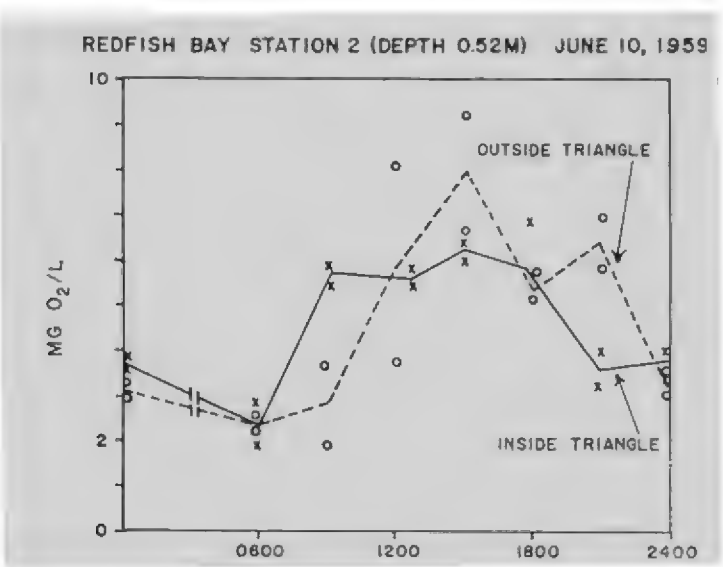

Fig. 20. Diurnal curves over turtle grass beds in Redfish Bay inside and outside a fiberglass enclosure, June 10, 1959. Salinity, 28 ‰; depth 0.5 m. Computations based on the inside curve yield: P, 5.9 gm/m²/day; R, 11.1 gm/m²/day. Computations from the outside curve are: P, 6.4 gm/m²/day; R, 11.8 gm/m²/day.

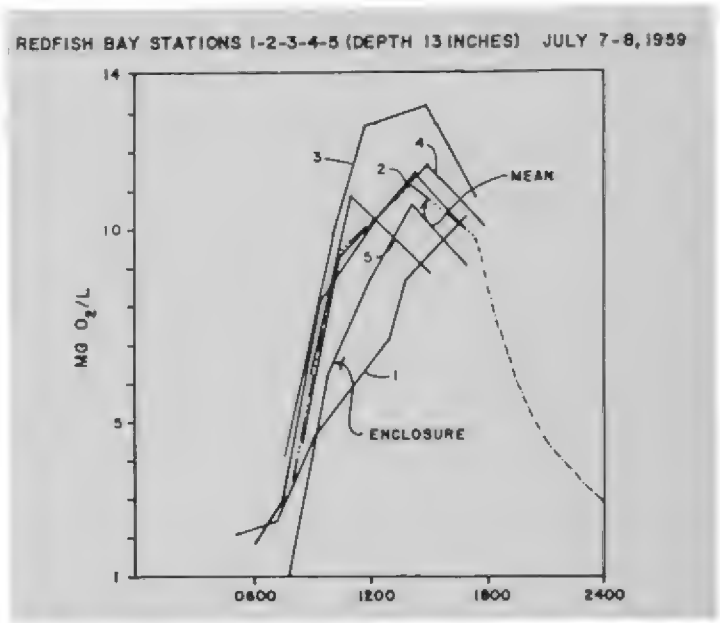

Fig. 21. Diurnal curves over turtle grass beds in Redfish Bay inside a fiberglass enclosure and in 5 outside stations July 7–8, 1959. In this figure each point is the mean of two separate Winkler analyses. Salinity, 32.8 ‰.

gm/m²/day) to that inside the enclosure (P, 5.9 gm/m²/day; R, 11.1 gm/m²/day). The graph for the outside water was slightly more irregular probably due to some heterogeneity of water drifting over the flats. Respiration exceeded gross photosynthesis on this day as throughout the season following the first dredging in March that released a light layer of turbid materials into the grassy areas. During this period the wind ranged from 5 to 18 miles per hour.

Later on July 7 during a period of extreme shallow water (0.3 m) in spite of difficulties in getting into the bay, measurements were taken at 5 bay stations and again in the enclosure. The data are indicated in Fig. 21 with each point based on duplicate samples. A computation for the whole bay based on the mean of all the data indicated a gross production of 13.8 gm/m²/day and respiration 12.3 gm/m²/day. The grass beds were prostrate preventing appreciable circulation. Temperatures in the afternoon reached 33–36°C. Oxygen levels were slightly lower in the enclosure especially at dawn indicating a slightly greater respiration relative to photosynthesis in the enclosure at this time, although production levels were still high.

These results indicate that enclosures can be placed over turtle grass beds for experimental purposes without immediately upsetting community metabolism.

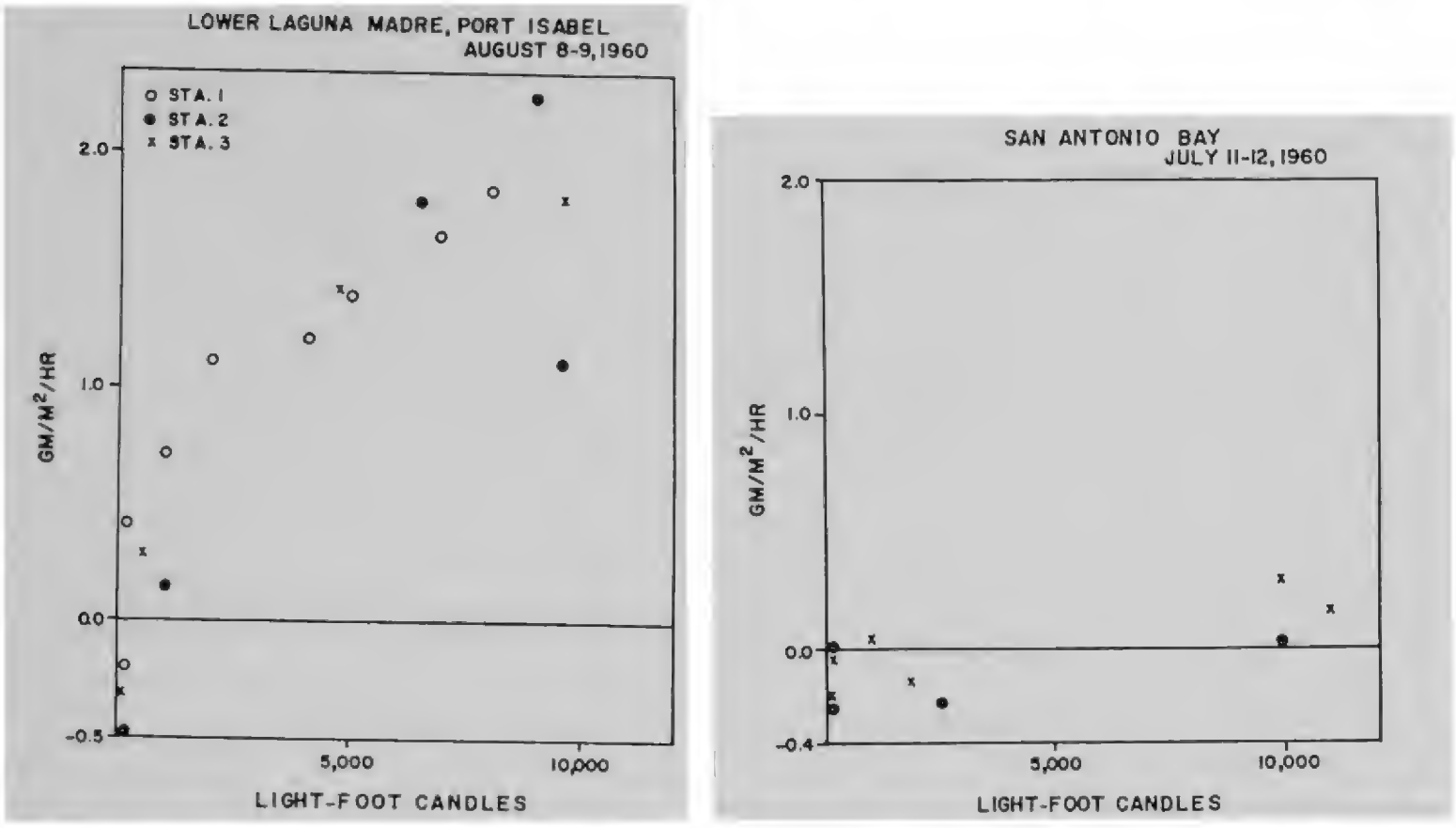

FIG. 22. Gross production as a function of light intensity in foot candles including data from different times of day. The left figure was taken from a grassy, relatively clear bay, Lower Laguna Madre, Aug. 8–9, 1960; the right figure was taken from a more turbid bay, San Antonio bay, July 11–12, 1960: solid circles, Hynes Landing; crosses, Gonzalez camp.

METABOLISM IN A LOUISIANA BAYOU

A pair of diurnal curves were made during sunny weather in a low salinity bayou at Hopedale, Louisiana, April 21, 1960 prior to dredging of the Mississippi River by-pass channel. The water in this area slides back and forth with the tide through small brackish lakes and channels among islands of marsh grass. One curve was taken at the margin of open water of Lake Borgne at about 1 ‰ and the other in Hopedale slightly more seaward at high salinity of 5–6 ‰. The oxygen change diurnally was very slight in both curves. Although the graphs were not as regular as those in more homogeneously mixed bays, there can be no doubt about the small amplitude of the metabolism. Computing metabolism for an average depth of 2 m, gross photosynthesis values found were 1.8 and 2.6 gm/m²/day; respiration values were 3.8 and 2.4 gm/m²/day. The waters were turbid with detritus from the marshes. The conditions were apparently similar to those extensively studied at the University of Georgia Marine Laboratory in which metabolism in the water was much less than that of the above-water marshes and dependent upon it (Ragotzkie, 1959).

Discussion

From the case histories presented in the previous section one may draw some inferences about the role of environmental factors in controlling the overall metabolism of estuarine ecosystems.

THE ROLE OF LIGHT, EFFICIENCY

The close correspondence between the diurnal variation in light and the diurnal variation in photosynthesis was illustrated in the previous paper (Odum and Hoskin, 1958).

Further evidence may be found in the 123 additional diurnal curves of photosynthesis, which have the general hump shape of the incident light. The sequence of productivity during passage of the clouded cold frontal zone during a time of relatively high productivity in May (Fig. 10) and the sequence of productivity on successive clear and cloudy days further indicate the close correspondence of oxygen production as measured in the free water and the incident light energy.

To further analyze the relationship of bay photosynthesis to bay light intensity, graphs were drawn of hourly photosynthesis as a function of light intensity as measured with a General Electric exposure meter with a foot-candle scale in the field (Fig. 22). The increase of efficiency with decrease of light intensity familiar in physiological studies of single plants is again verified as characteristic of whole ecosystems (Odum, McConnell, and Abbott, 1958). As discussed in the previous paper, as implied from free water data discussed by Verduin (1957), and as found in microcosm studies by Beyers (1961) the efficiencies in the morning are somewhat higher than in the late afternoon. This may be due to the diminishing nutrients available late in the day as demonstrated for phosphorus in these same bays by Bruce and Hood (1959).

Although one might expect a sewage lagoon (Fig. 16) with high nutrient levels to attain maximum possible efficiency in utilization of light, it may be noted that the natural and unpolluted grass flat systems of the Laguna Madre (Table 1 and Fig. 5, 7, 20, 21 and 22) have metabolism as high as the sewage lagoons. Where gross photosynthesis reaches a maximum at about 40 gm/m^2/day in either a grass flat or sewage lagoon in south Texas in summer, the efficiency of utilization of light energy in available wave lengths is about 6%, based on usable incident radiation of 2850 kg/cal and an approximate conversion of 4 kg-cal/gm oxygen metabolized. Thus both the man made system which was started with abundant nutrients and the natural system that accumulated its own necessary nutrients in a system of geochemical recycling were equally efficient. These efficiencies are similar to those attained in other communities of maximum output elsewhere in the world, the coral reefs, the agriculture of maximum fertilization, the rain forest, the Silver Springs system and others (Odum and Odum, 1960).

Since the photosynthetic output is dependent on incident light reaching the plant cells, the amount of absorption and scattering by turbid materials and water controls the productivity. The higher yields of the relatively clear front bays as compared to the turbid back bays may be related to differences in light energy reaching plant cells. Note photosynthesis at the same light intensity comparing the lower Laguna and San Antonio bay (Fig. 22).

In Fig. 23 are plotted representative graphs of penetration of light with depth. In the very turbid back bays such as Baffin and Copano bay the bay bottoms, although shallow, are illuminated with less than 1% of surface light intensity. The very clear lower Laguna allows more light penetration than Gulf waters at times.

For plankton systems importance of the depth of the mixing layer as compared to the depth of light penetration (euphotic zone) was quantitatively described by Sverdrup (1953) and applied to conditions in turbid estuaries at Sapelo island by Ragotzkie (1959). Where the depth of mixing is great enough to carry the plankton cells into the shade too long for cell photosynthesis to exceed cell attrition, the phytoplankton population cannot survive. The layer is said to be below critical depth. Thus, as waters get deeper, photosynthesis of the grassy-algal bottoms is replaced with a phytoplankton sys-

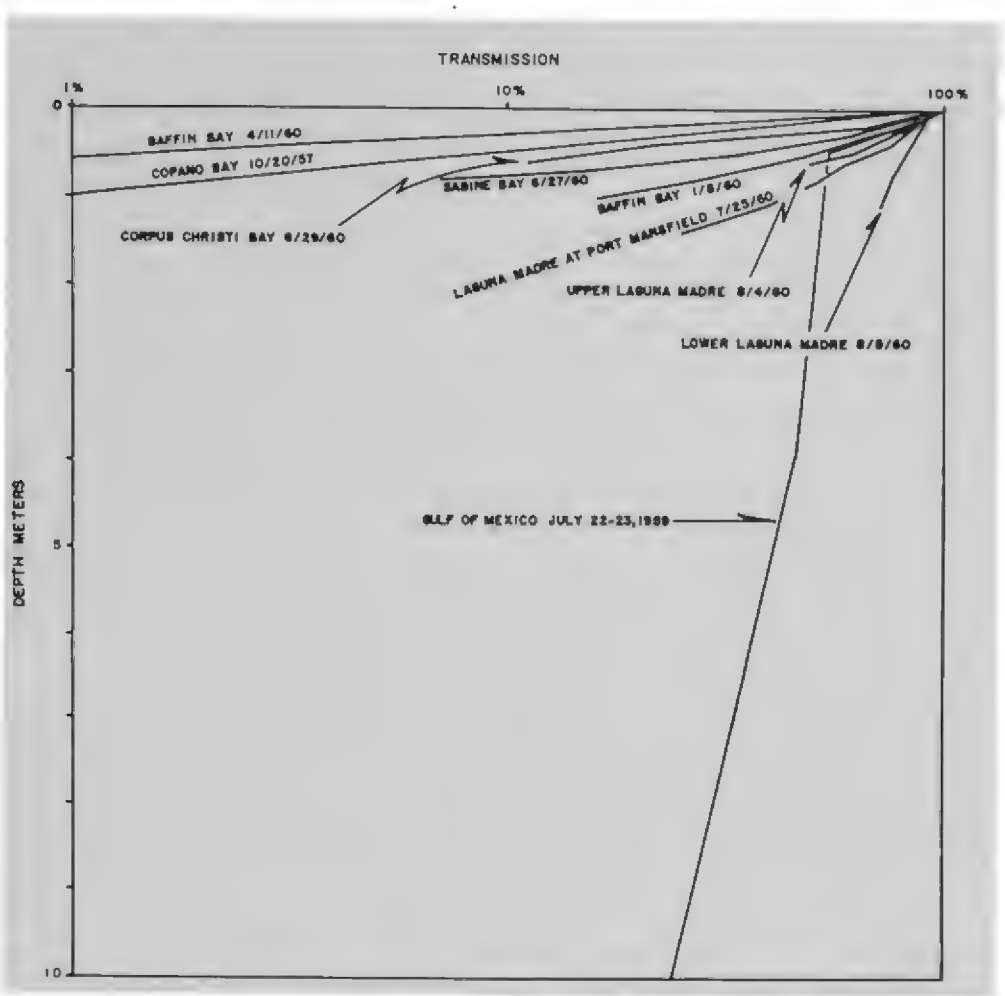

FIG. 23. Percent of surface visible light reaching bottom of Texas bays as a function of depth.

tem, and finally may practically disappear in turbid waters. Murphy (1962) has provided a graph quantitatively relating turbidity and depth according to the quantitative predictions of this theory.

Where the bottom is within the euphotic zone, high productivities are possible even with high turbidities. Waters circulating from deeper zones may not gain in net production except while they are passing over shallow bars. Under such circumstances the production of the whole bay may be a function of the ratio of area shallower than the critical depth to the area deeper than the critical depth.

Whereas turbidity is not disastrous in the shallow depths, it may essentially eliminate photosynthesis in the deeper waters. Fortunately, most of the bays of Texas are shallow enough and productive enough to be above the critical point much of the time. The first objective of any program for stimulating greater primary production in deeper Texas bays should be elimination of sources of turbidity.

THE ROLE OF TEMPERATURE AND COMMUNITY REGULATION

In the Texas bays both light and temperature undergo large annual and day to day variations between summer maxima and winter minima (Fig. 7). In Silver Springs, Florida, at constant temperature it was possible to attribute all of the annual range of photosynthetic production to the variation in incident light, but in the Texas bays some authors have been tempted to attribute some of the winter decline in biological stocks and activity to the decrease in temperature. What evidence there is, however, suggests a minor role for temperature. Low temperature (above freezing) does not in itself preclude high production rates. The basic photosynthetic process is not temperature dependent although temperature affects the output of whole plants studied (Stafelt, 1960).

High rates of photosynthetic and respiratory metabolism are known from adapted ecosystems in arctic climates in summer. Adaptations, successions, and evolutions in an ecosystem can occur to permit high metabolism at low temperature.

In the annual picture temperature does not begin to fall much until the cold fronts begin to pass through in November. The photosynthesis, however, begins to decline markedly (Fig. 7) as soon as the light income begins to decline in July.

As established by many authors the temperatures in the shallow bays follow that of the air masses that blow over them. There may be 15 degree centigrade range from one day to the next in winter. As illustrated in the case history presented for a February norther (Fig. 11), rapidly falling temperatures have a profound effect on the gas exchanges, but do not eliminate the metabolism.

The hypothesis is proposed that the system and its organisms are sufficiently organized in their activity to keep the total metabolism in phase with food conditions as developed seasonally from light energy. In the annual cycle the total community metabolism is somewhat independent of temperature. What proportion of this community regulatory activity may be controlled by the migratory behavior of populations and what proportion may take place within the physiological mechanisms of the single organisms is not known.

The diurnal range of temperature like the diurnal range of oxygen content is a function of the water depth with greater ranges in shallow water. In the water film communities the daytime temperature approaches the upper limit (40°C) for many organisms.

The Role of Turbid Bottom Materials

The release of turbid materials is a dominant feature of the Texas area with organic laden silts and clays released in large quantity into the bays from the rivers, from dredging, from reagitation up from the bottom during storms, and from beach erosion. Turbid materials had two distinct effects on total metabolism as observed in this study. One effect of turbidity in reducing light penetration and thus reducing primary production was discussed in the previous section on light. The other effect was a stimulation of the community respiration apparently due to organic matter accompanying the inorganic turbidity.

In the turbid water of Baffin Bay, in San Antonio Bay, during dredging in two places in Redfish Bay, in the floodwaters in Matagorda Bay, in the Louisiana bay at Hopedale receiving marsh detritus, and in the back bays receiving rivers, respiration was often in excess of photosynthesis suggesting that the import of organic matter was supporting consumption in addition to that produced by plants in situ. In Fig. 24 are data for the hypersaline Baffin Bay in which R exceeded P frequently, especially when salinities fell following rains. These days were like the waters of the Neuse River, North Carolina, in which respiration of a stream exceeded its photosynthesis with much of the consumption supported by organic matter running off the land (Hoskin, 1959). Similar conclusions were drawn by Pomeroy (1959), Ragotzkie (1959), and Teal (1959) in their studies of the metabolism of the Sapelo Island marsh waters.

Although respiration was in excess of production in turbid water studies, the excess was not a large one. In nature respiration was not in excess of photosynthesis by more than a factor of 2. Larger excesses of respiration over photosynthesis have been recorded in marine bays with known pollutions (Odum, 1960).

A complicating aspect of the additions of turbid matter is the stimulus provided to photosynthesis indirectly through the excess of respiration over photosynthesis. Where R is in excess of P, inorganic nutrients accumulate stimulating photosynthesis. Thus the turbid mixtures of organic and inorganic matter both interfere with photosynthesis by shielding light and stimulate it by indirectly raising inorganic nutrient levels.

Studies by Wilson (1961) with the infra-red CO_2 analyzer method for assay of dissolved and suspended organic matter have demonstrated the relatively high concentrations of organic matter found in the Texas bays with greatest concentrations up to 80 mg/l in the turbid back bays so far studied including Baffin and Corpus Christi bays. Excess respiration over photosynthesis of 5 mg/l/day (Fig. 24) would consmue a stor-

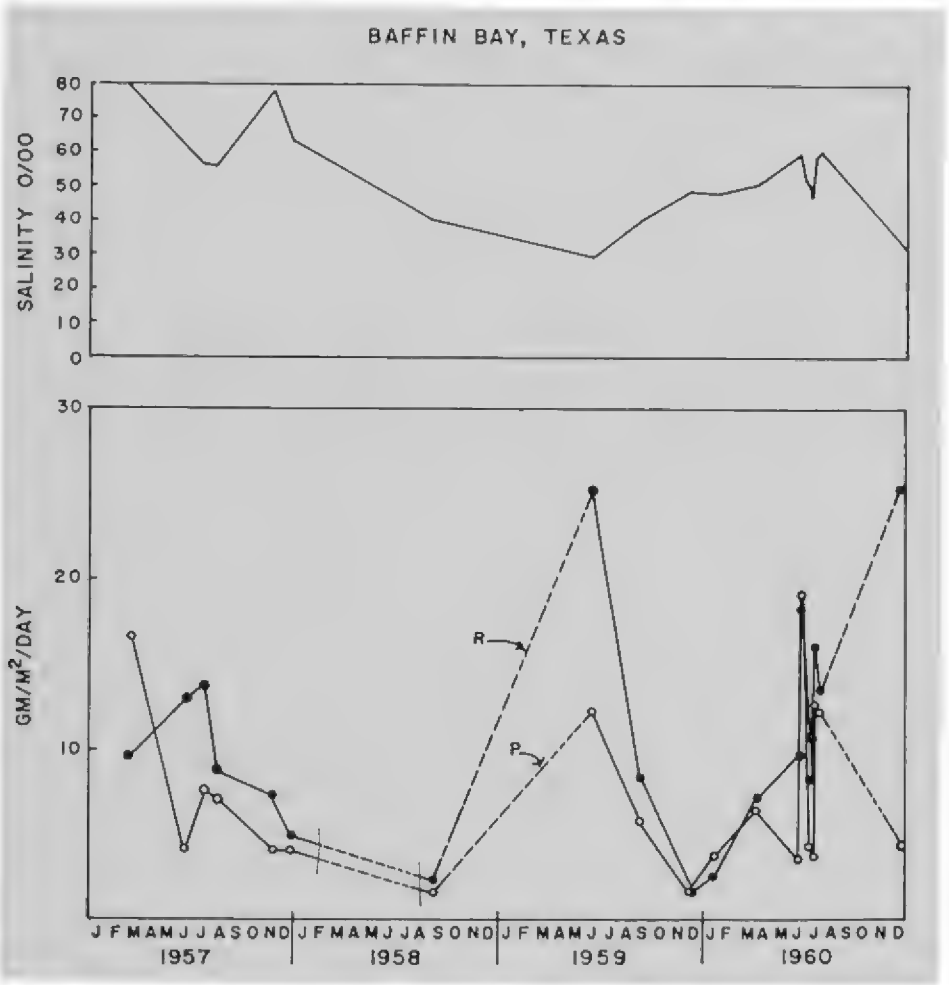

FIG. 24. Metabolic data from Baffin Bay, Texas, during dry and wet periods.

age of 80 ppm in about 16 days, but there is rarely decrease in respiration relative to photosynthesis. Apparently the inflow of extra-bay organic matter is keeping up with the consumption since the organic levels and excess respiration over photosynthesis are maintained particularly when the salinity is falling.

THE ROLE OF AREA AND AGITATION

Physical circulation is a normal requirement for many ecosystems supplying the nutrients for photosynthesis and redistributing the organic matter and oxygen as fuel for consumers. In the Texas bays the areal extent determines the amount of circulation that can develop under the strong winds usual for the area.

Armstrong Price (1947) and others have discussed the area of the bays as a controlling factor on the depth of the bottom. They indicate that in small bays, insufficient wave energy develops to keep the bottoms from filling in with sediment to shallow levels. In deep bays mixing favorable to photosynthesis is partially offset by greater equilib-

rium depth maintained by scouring in the larger bays. The role of agitation on metabolism is further masked by the rapid settling of the turbid materials during periods of relatively calm weather, when the additional penetration of light tends to offset any unfavorable aspect of diminished circulation. With the interplay of factors of area and agitation it is not easy to select natural experiments that delimit the factors.

A comparison may be made between the metabolism in the small shallow sloughs (Table 1) as compared with the larger but equally shallow bays like the Laguna Madre (Table 1, Fig. 7). Similarly metabolism of enclosed and less agitated boat harbors may be compared with that of the open, well mixed bays (Table 1) of similar depth.

In general the small littoral bodies of water, sloughs, and harbors, in spite of opportunities for nutrient supplement from littoral pollutions did not sustain greater production and metabolism than the larger wind-stirred, freely mixing bays.

The Role of Nutrients

It is axiomatic that the maintenance of an adequate nutrient supply is essential to the maintenance of maximum gross production. Maintenance of nutrients is accomplished in some systems by the recycling of nutrients from the respiratory consumers. In some systems nutrients are regularly imported balancing those lost. Pomeroy, working in the estuary of the Altamaha river in Georgia (Pomeroy, 1960) showed that where bays receive flushing out of water with floods of low-nutrient, fresh water; accumulated nutrients tend to be flushed out. Such floods also kill off many of the larger organisms so that their stored nutrients are also lost. Hoese (1960) documented a case of such flushing for Mesquite bay.

In Texas bays studied it may be useful to propose three types of systems operating to supply adequate nutrients for high production rates: (a) hypersaline regimes, (b) bottom grass-algal systems, (c) systems near inflows of high nutrient concentrations.

(a) In the high salinity bays, the Laguna Madre and Baffin bay, after long periods of sustained high salinity, nutrients have an opportunity to be accumulated and recycled. As indicated in Table 2, high values of total phosphorus, 2 to 3 mg-atom/m^3, occur in

Table 2 Total phosphorus in Texas bays.
Groups of analyses are arranged in order of decreasing salinity.
Analyses by H. Bruce, R. Ward, and C. Oppenheimer

	Number of samples	mg-atom/m^3
HYPERSALINE BAYS, salinity, 50 to 70‰		
Baffin Bay, July 26, 1957	8	2.7–5.2
Baffin Bay, August 15, 1957	9	3.4–4.2
Upper Laguna Madre, July 23, 1957	4	1.4–3.2
Upper Laguna Madre, August 1, 1957	8	3.4–4.2
GULF OF MEXICO, salinity, 33 to 36‰		
Port Aransas jetties, July 15, 1957	8	2.0–2.2
Port Aransas jetties, July 23, 1957	1	1.8
Whistling buoy, Port Aransas, August 10, 1959	4	0.0–1.27
BOAT HARBORS, salinity, 28 to 34‰		
Corpus Christi T head Harbor, August 10, 1959	2	1.6–1.9
Rockport Basin, August 5, 1957	8	2.0–4.0
GRASS FLATS, salinity, 29 to 33‰		
Redfish bay, July 17, 1957	1	1.3
Redfish bay, August 10, 1959	8	0.62–1.38
PLANKTONIC BAY, TURBID, salinity, 10 to 28‰		
Copano Bay, August 8, 1957	8	1.6–2.4
Corpus Christi Bay, July 23, 1957	3	1.2–1.9
Corpus Christi Bay, August 10, 1959	6	0.80–0.97

dry years. The details of the daily uptake and regeneration have been shown by Bruce and Hood (1959). A similar high nutrient state has been established for inland waters in arid climates (Hutchinson, 1957).

Bays that are stable with little flushing are the ones thought to develop higher productivity and nutrients self-regenerated.

(b) In shallow water where bottom communities of grass and attached algae dominate the metabolism, flushing out of water due to floods or due to winter northers that drop the Gulf level are not so serious as in deeper bays, for much of the nutrient reservoir is not in the plankton but in the attached bottom materials. Providing the flushing does not kill the bottom system, the ecosystem can conserve nutrients for sustained high production.

(c) Where high nutrient levels in usable proportions are maintained in the inflowing water, flushing may not be detrimental to nutrient supplies. Nueces Bay and Oso Bay are examples of areas that often receive high nutrient contents due to municipal and industrial effluents.

It is not always possible in field analyses to show when nutrients levels are limiting metabolism or when the reverse is actually the initial cause and effect (inadequate biota and metabolism for storage and circulation of nutrients). If the production is limited by some non-nutrient factor, the impoverished biota may be unable to store high concentrations of nutrients in the geochemical recycling system. In any case, however, the nutrient level may be correlated with the gross production. In Table 2 the higher values of total phosphorus were associated with the areas of higher production in Baffin Bay and Laguna Madre whereas lower values, about one mg-atom/m^3, were found in Corpus Christi Bay.

As the many experiments on ponds indicate (Barrett, 1953; Hepher, 1959), adding concentrations of a nutrient like phosphorus may not have a sustained effect in many instances longer than the time for immediate uptake by the plants. The increase in photosynthesis in the fertilized slough (Table 1) followed by a decline in metabolism in subsequent weeks seemed to follow this pattern. Sustained increases in production require maintaining high rates of nutrient conservation and regeneration. Spot fertilization of the bays of Texas is likely to have the temporary effects found in fishpond work, but large sustained increases in fertility involve developing the nutrient conservation system like those already effective in some bays. Possible measures include development of hypersalinity by diversion of runoffs, the development of more grass flats by control of turbidity and depth, and the channeling of nutrients of municipality and industry into areas to balance rate of flushout.

The photosynthesis in the unfertilized natural grass beds around Port Mansfield (Table 1) was greater than the photosynthesis in the beds around the sewage outfall in Laguna grass flats near Ransom Island. It is doubtful if one can stimulate metabolism much by fertilizing an ecosystem if it already has P equal to R and a fully developed standing crop in stable steady state, geochemically recycling nutrients at rates equal to the maximum photosynthetic demand possible at the available light intensity.

For most of the Texas bays there is considerable opportunity to increase total production and consumption by changing the regime for nutrient supply. There is no reason why diversion of the flushing floods and sustained fertilization cannot maintain many bays much closer to the maximum productivities observed in the lower Laguna Madre

in 1960. Such an action program may be expected to double biological output of a half million acres.

Potential Yields

The measurements of gross photosynthesis indicate the effectiveness of light in producing organic matter. In the natural aquatic communities of Texas P and R are often similar, and there is little net gain or loss of organic matter except for fish migrations and detritus export to the open Gulf. This balanced pattern may be changed by artificial management. If means similar to those of terrestrial agriculture can be employed to reduce respiration by weeding of consumers and if outside nutrients are added at a rate adequate to replace the normal supply from respiratory regeneration, then a great part of the gross production might be channeled into organic storage for harvest. Since the rates of maximum gross photosynthesis measured in the Texas bays are equivalent to maximum rates of gross photosynthesis in agriculture, the potentials for eventful harvest and use are about the same.

The grass flats because of their stability, nutrients conservation, and ease of manipulation can be the first of the large marine systems to be managed commercially either for increased fisheries and wildlife or for organized aquatic agriculture, harvesting plant matter.

In arid areas along sea coasts the farming of the sea waters has the advantage over terrestrial agriculture in not being limited by water shortage. The bay waters of arid south Texas are suitable for providing world leadership in management of marine waters for useful purposes.

Summary

1. Further studies were made on the photosynthesis and respiratory metabolism of the marine bays of Texas with the diurnal oxygen method. On the basis of 123 new curves, the characteristics of metabolism of the planktonic and grassy bays have been explored with emphasis on refinement of methods, natural experiments, and special situations. Measurements were included from 9 bays not heretofore studied metabolically. The bays included in this study are all continuously well mixed by the winds without vertical stratifications.

2. Photosynthesis and respiration were generally similar and often in phase although the annual metabolism in single bays ranged from 0.5 gm/m^2/day minimum in winter to 40 gm/m^2/day maximum in summer.

3. In the back bays receiving runoff, respiration often exceeded photosynthesis. Such conditions existed in low salinity bays and also in hypersaline bays after rains.

4. In bays where P and R were equal total metabolism was often greater than where P and R were not in balance and where one or the other part of the nutrient cycle between P and R may have been limiting. Metabolism and phosphorus levels were higher in hypersaline bays in which there was little flushing out by rivers.

5. The reaeration constant as computed from diurnal graphs were related to depth and wind velocity. The area-based reaeration constant K increased with water depth from about 0.1 gm/m^2/hr at 10 cm depth to 5 gm/m^2/hr/100% deficit in bays 4 m deep. The volume based reaeration constant k was fairly constant with depth, about

1.0 gm/l/hr/100% deficit. Reaeration was surprisingly unimportant in the shallowest film communities measured.

6. The volume based reaeration constant increases with wind velocity by a factor of at least 2.

7. Several refinements in the diurnal graphic analyses were introduced to increase accuracy and avoid recurring artifacts. A photosynthetic bulge after sunset was found on many rate graphs of diurnal analysis and identified as an artifact due to seabreeze effects, easily recognizable from data on wind velocities and a convex shape of the post-sunset oxygen graph.

8. Inferences were drawn from studies of particular case histories. Dredging produced a condition in which R exceeded P during dredging. After the shading of the turbidity disappeared, P was equal or higher than before. Respiration was also increased when strong winds stirred the bottom in a tropical storm.

9. The small shallow sloughs and pools isolated from the main bays contained tremendous ranges of diurnal temperature and oxygen content, but on an area basis only one receiving pollutants was as productive and metabolic as the best developed, larger, grassy bays. Film communities went anaerobic at night and developed blue-green algal mats.

10. Some of the graphs indicated a greater respiratory metabolism of oxygen just after dark than before dawn, suggesting diurnal rhythm of respiration related to the photosynthetic output. Efficiency of photosynthesis was slightly greater just after dawn than just before sunset suggesting the stimulatory effect of nighttime R on P.

11. Hexadecanol on two sloughs was temporary in effect and did not greatly affect the diffusion constant or metabolism.

12. A boat basin with active operations of small boats retained apparently near-normal photosynthetic and respiratory metabolism without going anaerobic at any time of night.

13. One sequence of diurnal data from the turbid, low salinity bayous in Louisiana marsh lands indicated a relatively low photosynthesis and respiration in April.

14. An enclosure with fiberglass walls placed over a turtle grass bed for experimental purposes did not immediately disrupt photosynthesis and respiratory metabolism.

15. In representative Texas bays the light of visible wave lengths suitable for photosynthesis penetrating to the bottom averaged about 36% of surface intensity. Turbidities as indicated by extinction coefficients per meter for a visible range photometer without filters ranged from 7.7 per m in turbid back bays to 0.33 in the lower Laguna Madre at Brownsville and 0.11 on the Gulf shelf off Port Aransas. In most bays the critical depth for phytoplankton growth was not often exceeded.

16. A close hour by hour correlation of photosynthesis with light intensity was observed in the daily measurements during passage of fronts, or in comparisons of successive clear and cloudy days. Turbid bays contained much less photosynthesis than some clear bays at similar light intensity.

17. The graph of photosynthesis versus light intensity was without a light saturation point. High efficiency was found at low light intensity, but maximum gross production was found at maximum light intensity.

18. Maximum efficiencies, productivities, and sustained respiration were found in natural, high salinity, grass flat systems with values equal to those in artificial sewage ponds. Values were as great as in tropical reefs with photosynthetic efficiencies as high as other aquatic communities of maximum fertility on earth.

19. To produce maximum total photosynthesis in all of the waters of Texas, measures for management should include: reducing turbidity, eliminating irregular flushing of flood waters, developing grass bottoms, retaining wind driven circulation, and adjusting water depths of shallow and deep areas towards an average depth of 0.5 m.

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Some Bacterial Populations in Turbid and Clear Sea Water Near Port Aransas, Texas

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Abstract

Direct counts were made of bacteria in clear and turbid sea waters near Port Aransas, Texas including waters of the Gulf beach, the Laguna Madre, and the Redfish Bay turtle grass areas. Counts ranged from 900,000 per ml outside the Gulf surf to 28,800,000 in turbid water along the shore of Redfish Bay. Counts were used to estimate bacterial biomass (0.2 to 6 g/m^3) and potential oxygen demand.

Introduction

The extensive, shallow, marine bay system of the Central Texas coast and the Gulf beach waters are noted for turbidity caused by the presence of clays, detritus, and living organisms. Visibility in the bay water is often limited to a few centimeters. Occasionally, for an unknown reason, portions of the bays become clear. At other times, e.g., after a storm, the water appears to be nearly a colloidal sol because of the high content of particulate material in suspension. The suspended material slowly settles out during quiescent periods and becomes resuspended by wave action during wind storms. As a result, the gradual sloping beaches and areas with vegetation exposed at the water's edge have sediments of finer particles.

In May, 1958, experiments were conducted to determine the bacterial populations in turbid and clear water within the Central Texas bay system and in the surf zone of the Gulf of Mexico. Bacterial populations were measured by direct microscopic method.

Areas Sampled

Fig. 1 illustrates the general locality of investigation. Surf samples were taken from an area near Padre Island Park where the water was clear. Samples were collected from the active surf zone at the breaking point of the waves and just outside the surf zone in deeper water. A second series of samples was collected from the Laguna Madre area near Pita Island on the west edge of the bay taken at approximately: mid-depth (30 cm) near shoreline in turbid water over a bed of *Diplanthera;* mid-depth (30 cm) over a sandy beach in clear water; mid-depth (30 cm) in an area where bottom sediment was stirred up by wading during our collecting activities; and mid-depth (30 cm) in clear water at a sandy point. A third series of samples was taken along the west edge of Redfish Bay in a small cove: one sample was taken in very turbid water at mid-depth in an area where considerable amounts of decaying sea grass had been deposited on the bottom; one sample was taken in turbid water above a *Diplanthera* bed; one in clear

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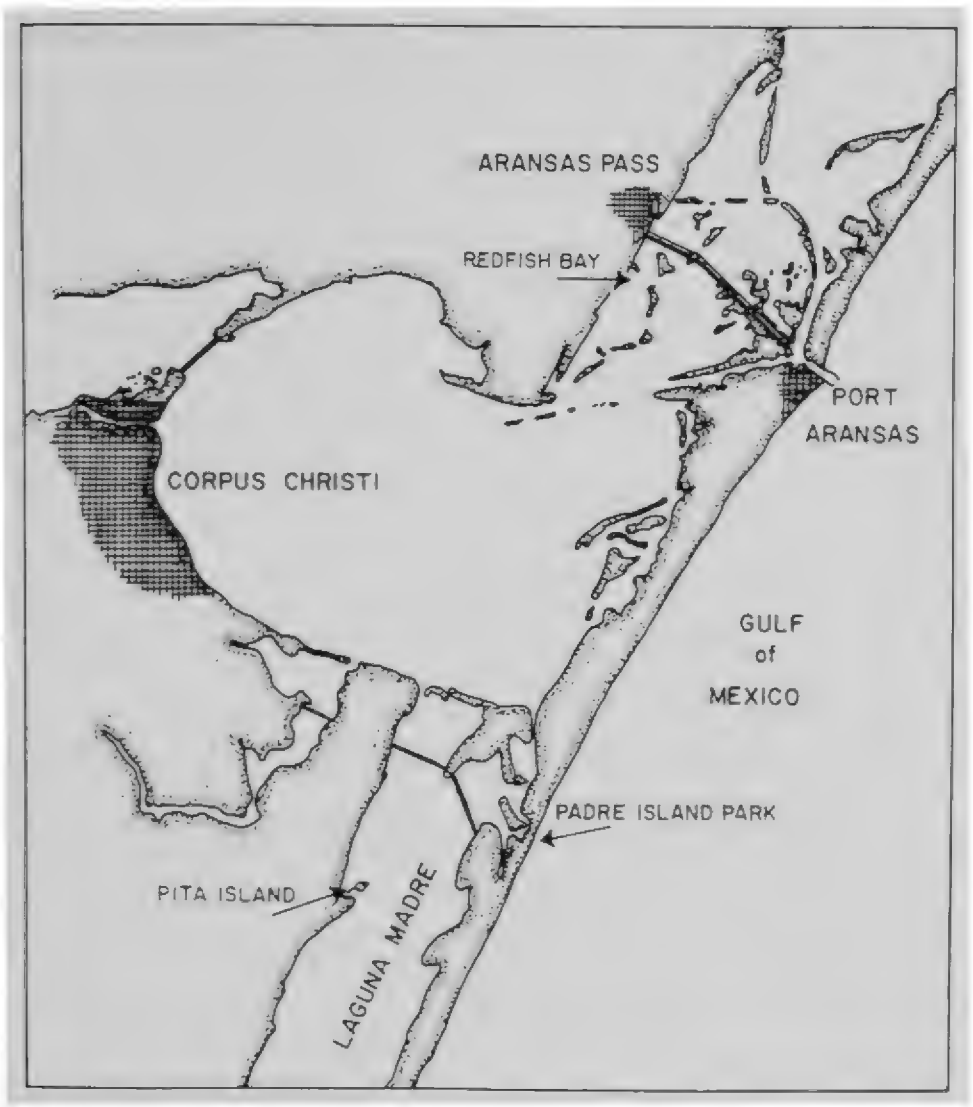

FIG. 1. Sample areas at Redfish Bay, Pita Island, and the beach of the Gulf of Mexico.

water over an attached *Thalassia* bed; and one near a sewage disposal outlet for part of the city of Aransas Pass.

The wind activity for the week prior to sampling was relatively quiet and the larger particulate materials had settled out. The average tide was estimated at about 10 cm. The turbid waters had small particulate materials which had not settled out or were colloidal in nature. The clear areas were typical of portions of the bays with large amounts of benthic plants and water less than 60 cm in depth. At present the authors have found no literature describing the colloidal aspects of turbid water in these shallow marine bays. Collier and Hedgpeth (1950) described some hydrographic conditions, and Shepard and Moore (1955) have reported hydrographical and geological details of the area.

Procedure for Direct Microscopic Counts

Bay water was collected in 500 ml sterile bottles and immediately fixed with formalin at a final concentration of two per cent. Formalin treated samples were analyzed at the Institute of Marine Science at Port Aransas. Direct counts were determined by a modified Cholodny technique presented by Jannasch and Jones (1959). Duplicate aliquots of 50 to 200 ml samples (depending on the turbidity) were concentrated to less than 5 ml but not to dryness with a millipore filter apparatus. The millipore filter retained particles of 0.4 microns and larger. The concentrate was placed in a small glass vial and filled with filtered distilled water to 5 ml volume. Duplicate aliquots of 0.01 ml of the concentrate were pipetted onto clean glass slides. The round drop, formed on the slide,

was dried in air and stained for 12 hours with a filtered mixture of two per cent aqueous erythrosin and five per cent phenol. The slides were washed with distilled water and dried at room temperature.

Direct bacteria counts were made with a Reichert Anoptral phase microscope to aid in the recognition of bacteria. Sufficient fields were counted to provide a calculated statistical variance of less than five per cent. Different morphological types of bacteria were tabulated during the counting procedure. Total numbers of bacteria were calculated from values for the area of each sample spot on the slides and the area of the microscopic field (average number of bacteria per microscopic field multiplied by the concentration factor). Biomass was calculated using the mass 2×10^{-13} g for one bacterium as taken from Kriss (1959b).

Results and Discussion

The bacterial numbers found in the samples are reported in Table 1. Bacteria must constitute a considerable fraction of the total particulate load in the waters of the bays. Unfortunately the total particulate load in the water was not measured at the time of the experiments. However a particulate load of 39.9 g/m^3 (dry wt) has been recently found in water near the Institute of Marine Science. The amount of dry bacterial mass (corrected for water content by assuming the bacteria to be 80 per cent water) in Redfish Bay sample 1 is 1.16 g/m^3. If the values for biomass and particulate load are compared, the bacteria represent approximately 3 per cent of the total load. In addition we can calculate approximately the total organic carbon supplied by the bacteria. Wilson (1961) gives an average organic carbon value of 4 g/m^3 for Redfish Bay water. Assuming that the bacteria are 5 per cent organic carbon, the 5.8 g/m^3 biomass found in sample 1 contains 0.29 g organic carbon/m^3. If the bacterial carbon is compared with Wilson's value, we find that 7.2 per cent of the total carbon is derived from bacteria. It is realized that these are rather gross assumptions but the values do give some concept of the importance of the bacteria under some conditions.

No significantly large differences were noted between bacterial numbers in clear and turbid water and the one Gulf sample. The Gulf sample outside the surf zone had the

TABLE 1

Average numbers of bacteria per ml and biomass by direct microscopic counts of water from shallow marine bays in May, 1958 from duplicate samples

Area	Water depth in cm	Average number of bacteria per ml	Biomass g/m^3
SURF GULF BEACH NEAR PADRE ISLAND PARK			
1 Surf zone	120	1,600,000	0.32
2 Outside surf zone clear water	180	900,000	0.18
PITA ISLAND, LAGUNA MADRE			
1 Near shore above *Diplanthera* bed, turbid water	91	9,000,000	1.8
2 Above sandy beach, clear water	60	20,000,000	4.0
3 In clear water	60	4,500,000	0.9
4 In the same clear water after sediment was stirred up by wading	60	52,000,000	10.4
REDFISH BAY			
1 Near edge in turbid water	60	28,800,000	5.8
2 Muddy water over *Diplanthera* beds	60	22,200,000	4.4
3 Clear water over *Thalassia* beds	60	2,700,000	0.54
4 Near sewage outfall, Aransas Pass	60	25,800,000	5.10

lowest bacterial population. The total biomass of bacteria is high for natural unpolluted marine waters as compared to the data of Kriss (1959a and 1959b) in the Pacific and Black Sea, and the data of Jannasch and Jones (1959). The bacterial biomass of our shallow bays is approximately 10 times the largest value given by Kriss for the Black Sea. The values in Table 1 do compare with those of Jannasch (1958) for Naples Harbor and ZoBell and Feltham (1942) for Mission Bay, California. It is interesting that coccoid forms apparently predominated in the bay waters at the time of collection (Table 2). Direct microscopic examinations of the sediments of the bays by the senior

TABLE 2

Percentage of types of bacteria

Area	Per cent of total			
	Rods	Spirilla	Vibrio	Cocci
1	0.9	0.7	1.3	97.1
2	0.2	0.3		99.5
3	1.7	0.2	1.3	95.5
4	2.9	0.3	1.3	95.5
5	1.0	0.1	0.2	98.7
6	0.9	0.2	2.3	96.6
7	1.9	0.2	0.8	97.1
8	1.6	0.6	1.9	95.9
9	4.8	1.3	1.0	92.9
10	3.4	2.5	3.2	90.9

author indicate that the rod shaped organisms predominate there.

During the stronger winds, from 20 to 60 mph, the surface sediment layers are mixed into the water by wave action. In clear water at Pita Island (Sample 3) the bacterial count was 4.5×10^6 per ml. When the surface sediments were mechanically mixed into the water, the count increased to 5.2×10^7.

The large indigenous populations may reflect large amounts of nutrients and a rapid potential metabolic activity. If one uses the general value of ZoBell (1946) for individual bacterial oxygen consumption (20.9×10^{-12} mg oxygen per cell per hr at 22°C) the calculated oxygen uptake at station 5 is 26 mg oxygen/l/day, assuming all bacteria to be active. One must realize, however, that although bacteria may be present, they are active only in the presence of food and favorable conditions. Living organisms which die may be immediately attacked by bacteria, and those bacteria which may have been in a resting state previously, immediately become active decomposers. Such a situation has been recorded by Oppenheimer (1960) where bacteria attach to dead but not living sedimentary diatoms.

The large bacterial populations and the high organic content of the bays (1 to 80 mg/l, Wilson, 1961) suggest the possibility of a large oxygen demand which may exceed the usual supply from atmospheric diffusion. If the bacteria were active and oxygen only available from photosynthesis and diffusion, one would expect the bays to become anaerobic at times. The senior author has not found anaerobic water conditions in unpolluted bays during three years of field investigations. The continual wind action over the shallow waters stirs the water, thus mixing oxygen from the surface. Mixing is a common occurrence, and salinity and temperature profiles are normally uniform except during tidal fluctuations near the pass entrances, after heavy rainfall, and during abrupt air temperature changes due to northers (Oppenheimer, Travis and Woodfin,

1961). The muds, often anaerobic at a depth of one centimeter (Oppenheimer, 1960), provide a poising capacity which may remove oxygen. Vertical mixing in the bays is very difficult to measure and correct. These speculations on potential oxygen consumption suggest a need for intensified research on metabolic activities during microbial decomposition.

Conclusions

Total numbers of bacteria, by direct counts in the areas studied, ranged from 900,000 to 52,000,000 per ml. The total bacterial biomass varied from 0.18 to 5.8 grams per m^3. Some difference was noted between adjacent clear and turbid areas. When the sediment was stirred into the water, the numbers increased approximately by one log number, increasing the biomass from 0.9 to 10.4 gm/m^3.

Acknowledgments

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Algal Mat Communities of *Lyngbya confervoides* (C. Agardh) Gomont[1]

LAZERN O. SORENSEN[2] WITH JOHN T. CONOVER[3]

Abstract

Studies of ecology, zonation, and growth were made of the extensive mats of blue-green algae, *Lyngbya confervoides* (C. Agardh) Gomont in the shallow lagoonal flats of bays in south Texas. Five zones were described in vertical profile, and microphotographs were made of representative filaments, including Zone A at the surface with dark sheaths, Zone C with thick clear sheaths, and Zone E with thin sheaths and contracted protoplasts.

Introduction

Algal mat communities in the Texas lagoons and mud flats in the vicinity of Mustang and Padre Islands, Texas (Fig. 1) develop in very shallow water from 1 to 50 centimeters deep. In some seasons the living mat is not covered by water and the organisms become dessicated. These algal mats occur in tidal basins, in small depressions near shore, and along most of the marginal borders of the broad lagoons. In these habitats

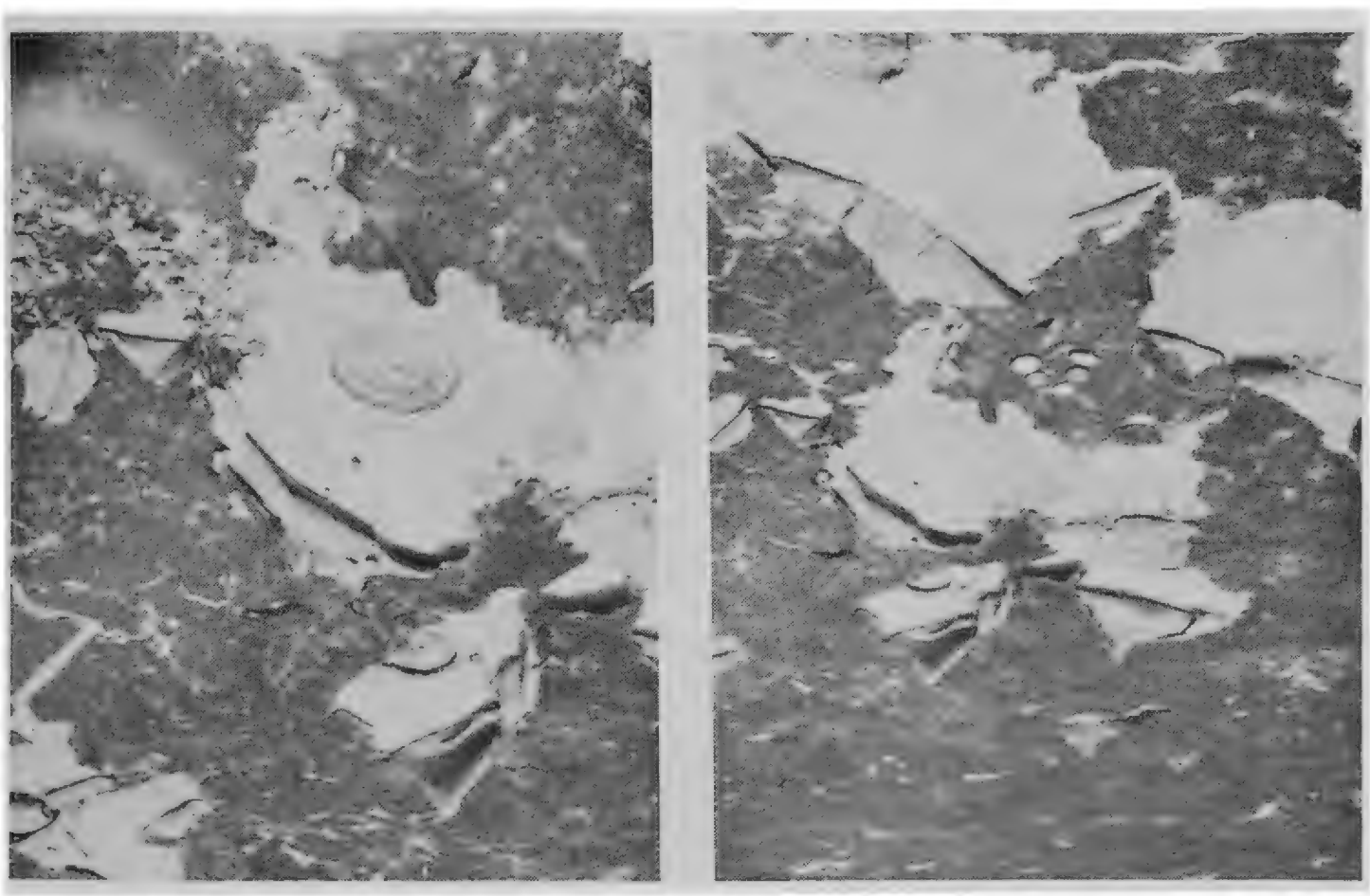

FIG. 1. Living algal mat on a mud flat near Port Aransas, Texas. Note varied layers of sediment in hole scooped out underneath the mat. Presumably these layers of organic matter represent former mat communities. The mat thickness here is about 1 cm. Photographs were taken in April.

[1] Based on observations at the Institute of Marine Science in summer 1959, with research stipends from The University of Texas.

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annual temperatures range from near freezing to 70° C and salinities from less than 1 per cent to over 20 per cent salt.

The living algal mats form papery crusts 1 to 20 millimeters in thickness. Examination of the microstructure reveals a laminar arrangement of living plants and animals. The list of organisms includes blue-green, unicellular green, flagellated and diatomaceous algae, bacteria, and a minor assemblage of worms, crustaceans and ciliates. According to Dr. H. Humm the biomass is largely made up of the filamentous blue-green algae, *Lyngbya confervoides* (C. Agardh) Gomont. In this report are data on microscopic details, growth, and vertical structure of the mat community.

The few available reports on algal mat communities have been descriptive. Ginsburg *et al.* (1954) compared living cyanophycean mat communities and laminated algal mat sediments with their fossil counterparts in the geologic record. These workers asserted that the important factors influencing mat growth were probably illumination, salinity, moisture, sediment (grain size), substrate (nutrients) and associated organisms, growth substances, etc. No experimental data were given to support these ideas. Breivik (1958) has described the microecology of mat and encrusting algal communities in the fjords of Stavanger, Norway. He gave no growth data.

Pomeroy (1959) studied the productivity of algal films in the salt marshes of Georgia at various seasons. He estimated an annual gross algal production of 200 g C/m^2. He found that factors which influenced production were light, temperature, pH, depth of flooding at high tide, and sedimentary chlorophyll. Light, he asserted, was the most important of these factors.

Living algal mats usually possess a dark brown to nearly black surface crust. Naegeli (1849) first called attention to the fact that the dark coloration was due to the staining of the sheaths of *Lyngbya* by some substance. Correns (1889), and Naumann (1919) identified this substance as a ferric colloidal complex in algal sheaths. More recently Kylin (1927, 1937) decided the pigment was possibly a hydroxide o firon to which he gave the name scytonemine. He suggested that the staining process may be the result of a photo-chemical reac:ion since it was associated with filaments exposed to direct sunlight and not with those in the shade.

If a sheet of living algal mat is sectioned, a laminar arrangement of the organisms can be seen in profile from the top crust to the bottom of the mat. The various layers observed differ in color and indeed in the composition of the community. Each layer has certain physical and biological features and may be traced in algal mats of geographically separate areas in the Texas lgoons. Apprently the Florida algal mats (Ginsburg *et al*, 1954) contain a different species composition but have zonation.

Dissection of the mat under a microscope reveals a darkly stained surface layer. Beneath the surface is a transitional zone which grades into a band of lustrous blue-green. In the lower portions of the mat are yellow and pinkish-yellow zones turning to a dirty yellow and finally merging into the black underlying sediment. For convenience in this paper the various color-defined zones, with their characteristic living communities have been labaled alphabetically from surface (A) to bottom (E).

Methods

Field measurements were taken of temperature, light, salinity, depth, and the nature of the community in each zone of the living mats of the lagoons. These data (Table 1)

TABLE 1

Characteristics of environment from which experimental material was obtained for experiments

Zone	A	B	C	D	E
Date	April 13–21	March 24–30	November 20–28	April 1–8	April 1–8
Temperature in °C	19–21	23–28	18–23	24–26	24–26
Salinity as per cent salt	8.0	4.3	4.1	9.6	9.6
Per cent of surface illumination	100	5	3.5	1.7	0
Total* illumination g cal per cm^2 per hr	95	80	65	110	100
Per cent free O_2 in air	100	<90	<50	<10	<1
Color of zone	Dark brown	Dusky blue-grn	Lustrous blue-grn	Yellowish blue-grn pink below	Pale yellow pink at top
Depth in mm	0–0.5	0.2–2	1–4	3–8	4–12

* Illumination given for 1 hour between 1200 and 1300 hours on an average day during the experiments. These data represent the highest illumination per hour hence greatest light penetration for each period.

provided the necessary information for simulating in laboratory cultures the environmental conditions of the lagoon mat communities.

The growth characteristics of each zone were examined by obtaining healthy samples of living mat from the lagoons and mud flats, peeling back the dark-stained surface crust, and teasing free samples from the mid-mat zones B, C, and D. The lustrous, vigorously growing blue-green algal filaments occur in these zones. The samples were grown in cultures (not pure) under simulated conditions for each zone, A through E (see Table 2).

TABLE 2

Experimental conditions during growth measurements in laboratory

Zone	A	B	C	D	E
Date	April 13–21	March 24–30	November 20–28	April 8–14	April 1–8
Temperature in °C	19–21	23–28	18–23	24–26	24–26
Salinity as per cent salt	2.6 for all gravimetric experiments 1.6 for all morphometric experiments				
Per cent of surface illumination	100	5	3.5	0	0
Total illumination g cal per cm^2 per hr	95	80	65	110	100
Per cent free O_2	21.0	<21.0	<10	0.05	<0.01
Per cent free N_2	78.0	>78.0	>85	99*	99*
Color of zone	Dark brown	Dusky blue-grn	Lustrous blue-grn	Yellowish blue-grn pink at bottom	Pale yellow pink at top

* 1% Argon.

Two types of experiments were performed. Gravimetric experiments were conducted using whole pieces of mat community including both plants and animals. These pieces were grown in cultures and their dry weight changes observed. Morphometric experiments were performed using isolated filaments of *Lyngbya confervoides*. These filaments were grown in impure drop cultures and their length changes observed.

In addition, especially for *Lyngbya* the laboratory cultures were compared quali-

tatively with lagoon mat samples. They were compared as to thickness and transparency of the sheath, predominating color of photosynthetic pigments, shape and graininess of the protoplast.

Six-liter glass dessicator jars were used as chambers in which the conditions of growth within the mat samples were simulated. A water bath was substituted for the dessicant to provide a water saturated atmosphere. The samples were placed into 1 cm deep clean plastic boxes on the ceramic shell of the dessicator and covered with natural pond water. Salt content of the pond water was 2.6 per cent.

The chamber used for growing cultures under aerobic conditions was fitted with a blotter-paper gasket between the lid and the jar. This gasket provided an exchange of air with the outside atmosphere but kept evaporation to a minimum. The blotter extending beyond the chamber reduced the sunlight falling on the cultures. By varying the width of the blotter, the amount of light reaching the cultures could be changed without altering the spectral composition.

The chambers for anaerobic studies were fitted with sealed lids. Oxygen-free nitrogen was used to replace air in the chambers. The gas in the chambers were tested before and after each experiment for the presence of oxygen using a Beckman GCl gas chromatograph. The cultures grown anaerobically were incubated in total darkness.

Duration of experiment, temperatures, illumination, and other conditions under which the cultures were grown are shown in Table 2.

The mat samples, used in the incubation chambers, were washed with tap water to remove soil, organic detritis, and larger metazoa. Examination of the washed and unwashed samples indicated that larger algae were retained intact when washed but some of the smaller living organisms were removed. The samples were then dried at 40°C for 24 hours. The gain or loss due to growth of the community was measured on this dry weight basis. Heat drying of the living mat at 40°C may have had little effect on the viability of most of the microorganisms, because organisms in natural mat communities are normally exposed to large changes in temperature and water content. When dried mat material was placed in pond water, algal filaments and bacteria began to show motility within one hour. Weight changes after the first two hours of imbibing water were negligible. Approximately 0.2 to 1.5 g dry weight samples were used for the experimental cultures.

Aliquot amounts of the natural pond water, containing organic compounds, were dried and the residue weighed. The dry weight of the pond water residue per volume used in the culture boxes was then subtracted from the final weight of the incubated samples. Protoplasmic weight increase by algal mat samples in excess of the pond water residue weight was interpreted as growth with carbon (CO_2) derived from the water and the chamber's atmosphere.

The growth increases in *Lyngbya confervoides*, the alga which comprised over 80 per cent of the living community in the mat (optical estimate), were obtained by morphometry. Single filaments of this blue-green alga were isolated with microdissecting needles, washed in several exchanges of distilled water and placed on clean microslides. A drop of filtered marine pond water (16‰ salinity) was added to the slide. A cover slip was carefully dropped over the water drop. A thin film of petroleum jelly was applied on the slide around the edge of the cover slip without sealing it to prevent loss of the filaments. Usually four to six filaments per slide were used.

At the beginning and end of each experiment the microslides containing the individual filaments were placed on the stage of a compound microscope and the filaments were projected by means of a mirror and strong light source and measured directly on a drawing board. It was usually possible to recognize individual filaments due to the presence of certain damaged cells, sheaths, artifacts, or other identifiable structures. The projected images of the trichomes within the sheaths were measured with a precision millimeter rule. Calibration of the images projected on the board was accomplished by establishing for each magnification used (400X and 1000X) the number of microns of microscopic field (obtained with a stage micrometer) per millimeter on the drawing board. A measuring error of plus or minus 0.005 mm was obtained by this method.

The slides containing algal filaments were floated on foam plastic in 5 mm deep water baths of distilled water inside small rectangular clear plastic boxes (6 cm × 12 cm × 2 cm) with tight fitting lids. Holes, bored one in each end of the lid and stoppered with corks were provided to flush out normal air and to replace it with nitrogen for anaerobic growth experiments. A small shell vial was placed inside the pill box and filled with boiled alkaline methylene blue indicator solution to show the presence of oxygen in anaerobic growth experiments. The lid of the box was sealed with a plastic clay substance used by electricians in place of insulation tape. Pill boxes used for aerobic growth studies were similar in design but the lids were not sealed. Cultures for morphometric studies were incubated only three days.

The buoyancy of hormogones was determined by placing a number of hormogones of four to ten cells each in three depression slide chambers. One depression slide was filled with fresh water and the others with salt water (3% and 20%). A cover slip was firmly sealed over the depression with petroleum jelly. The slides were turned end to end a few times to agitate the hormogones and placed vertically on the stage of a horizontally tilted compound microscope. This arrangement permitted gravity to settle negatively buoyant hormogones in the bottom of the depression slide while positively buoyant spores floated to the top. Counts were made of the number of hormogones which sank or floated. Empty sheaths and living filaments of *Lyngbya* were observed, using the same method.

Measurements of light penetration through layers of algal mat were made with a photometer with a selenium cell.

Results

Description of Algal Filaments from the Zones in the Mat

In Fig. 2–6 are presented microphotographs of algal filaments from the mat and those cultures in similar light regimes. Near the surface in zone A (Fig. 2) the algal sheaths are blackened giving the whole mat a darkened coloration.

In zone B there is a transition with loss of sheath coloration (Fig. 3).

Below in zone C, the sheaths are clear. Many hormogones were being formed. The protoplasts were fine grained. The filaments were lustrous blue-green with a brilliant color not seen above or below this zone (Fig. 4).

Under zone C, in zone D, 3 to 8 mm below the surface is a yellowish carotene-tinted layer with many dead sheaths, walls, remains of worms and crustaceans, increasing numbers of colorless flagellates and bacteria and some purple bacteria. The living filaments

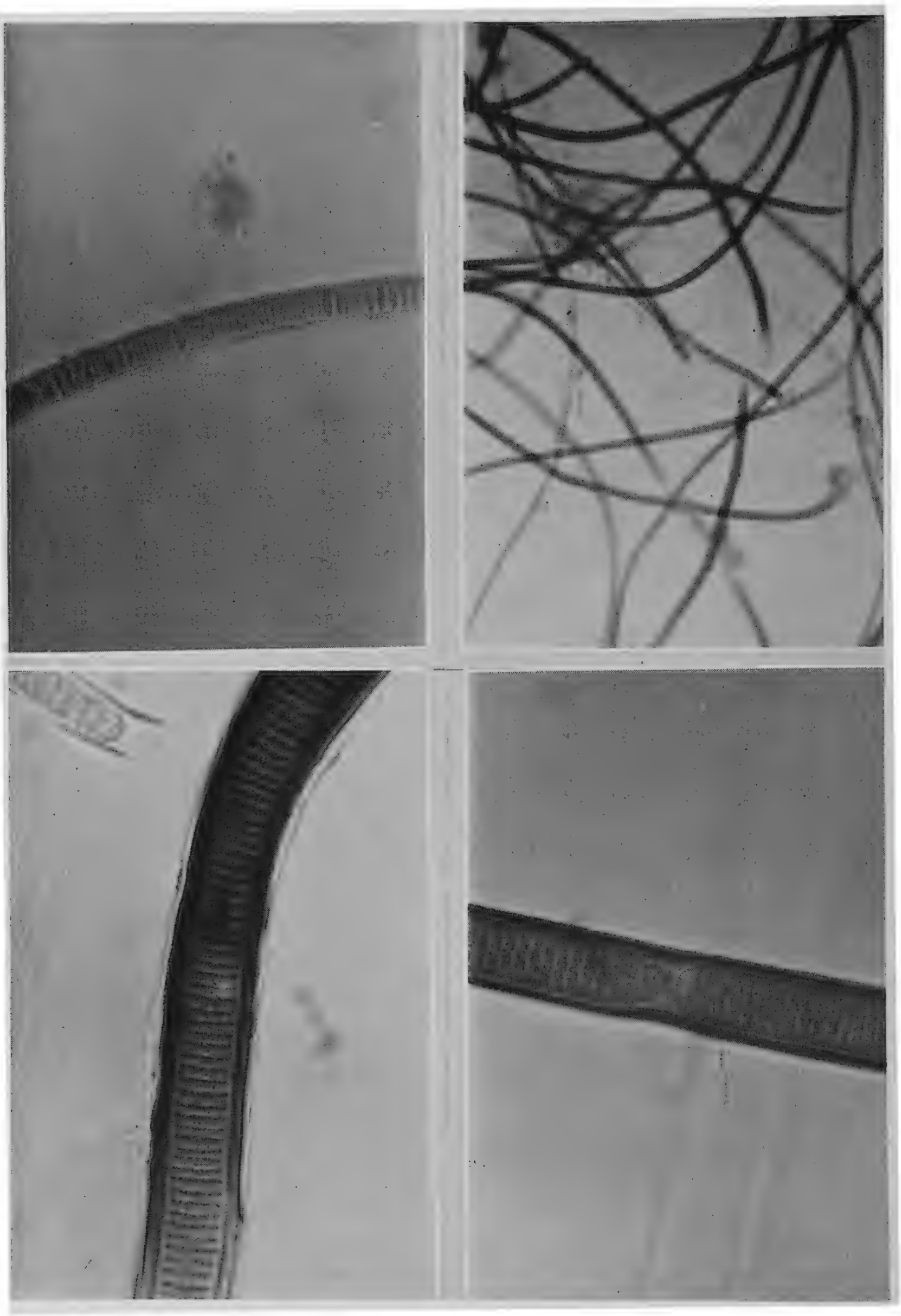

FIG. 2. Zone A. Photomicrographs of filaments of *Lyngbya confervoides* extracted from the surface crust of a mud flat algal mat designated as Zone A. Note the sheath coloration.

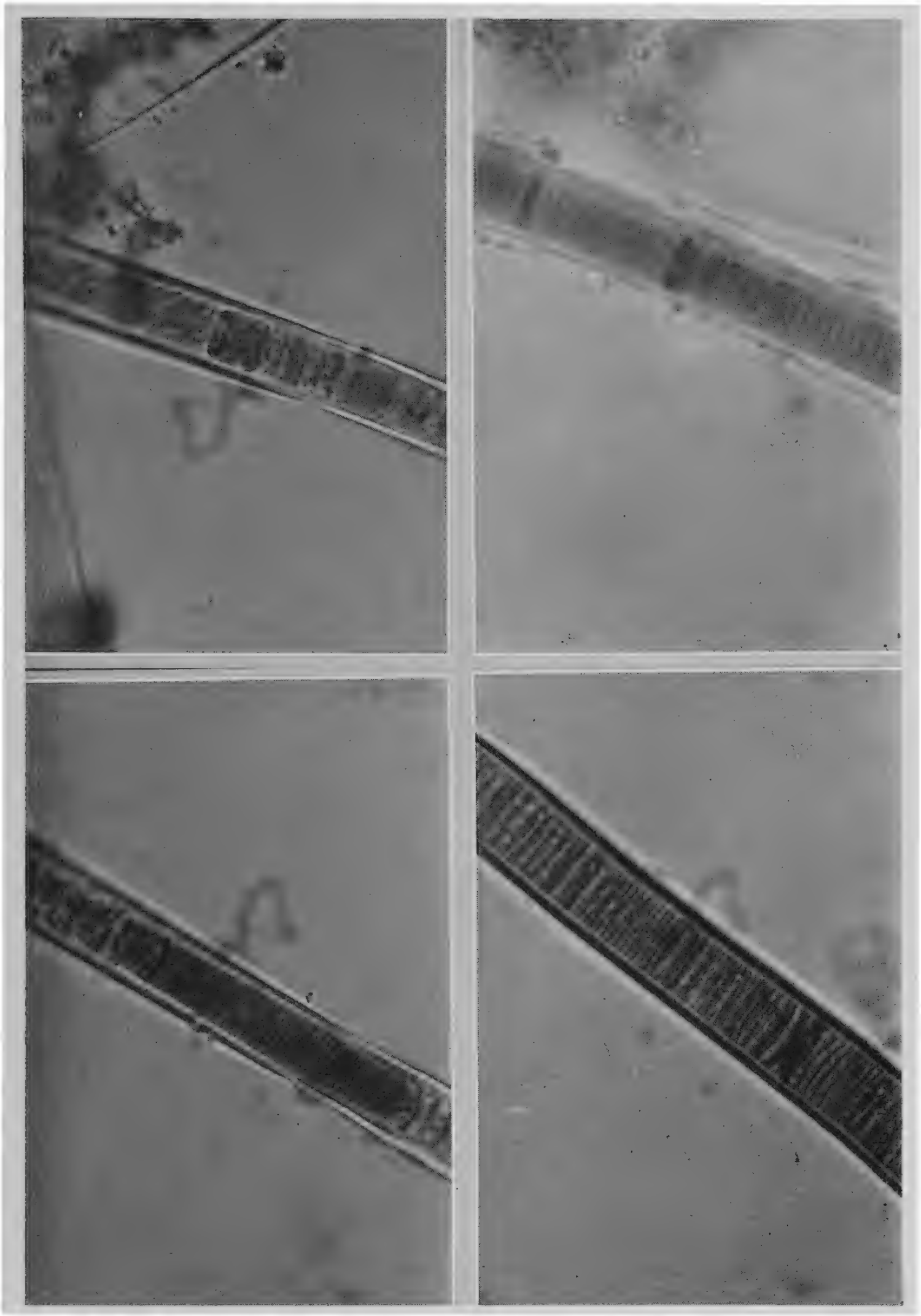

FIG. 3. Zone B. Photomicrographs of filaments of *Lyngbya confervoides* teased from the immediate subsurface layer, designated as Zone B. Note the thick sheaths, reduced opacity of the sheaths, and larger number of intact, unplasmolized cells.

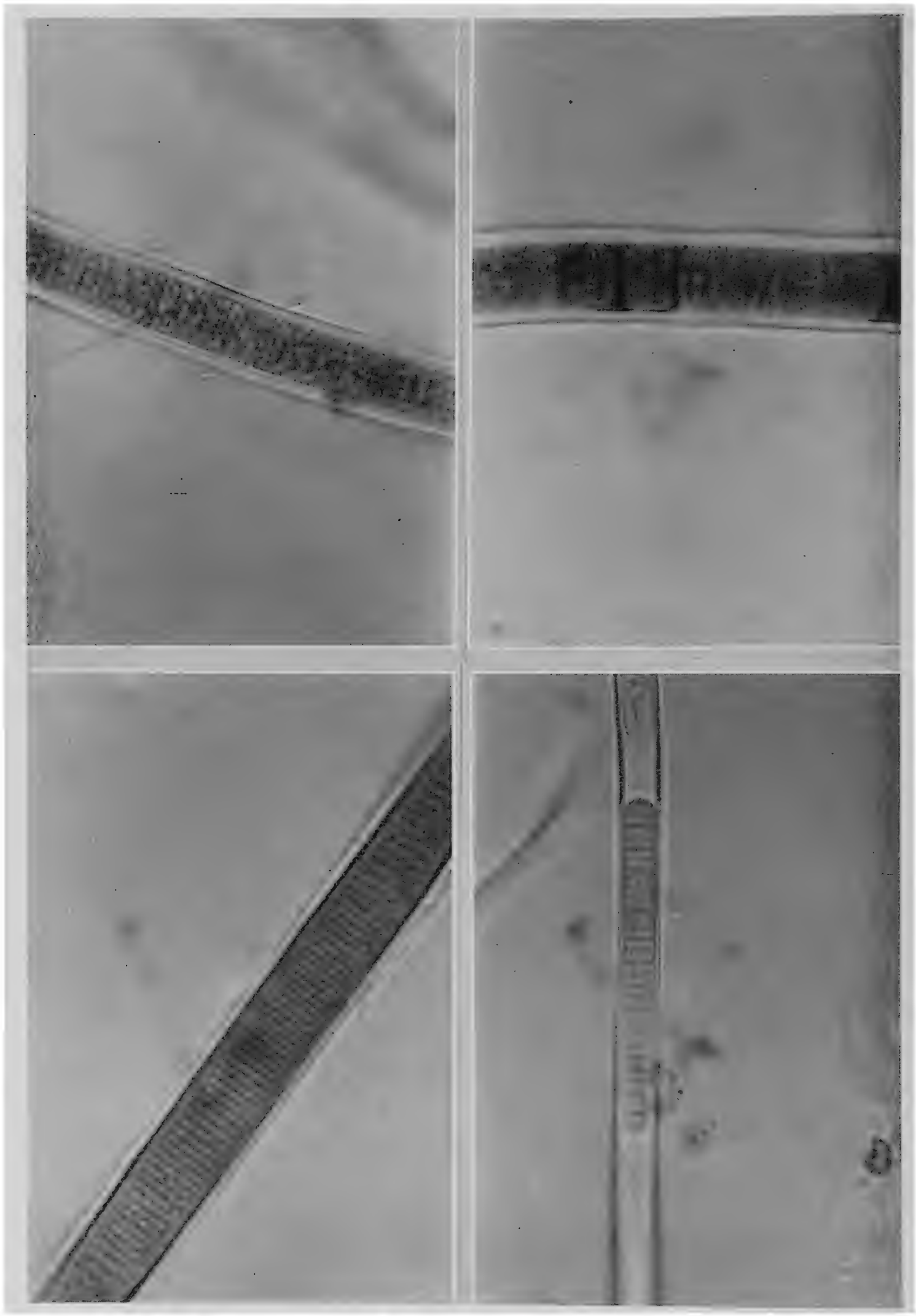

FIG. 4. Zone C. Photomicrographs of *Lyngbya confervoides* obtained from a mud flat algal mat. The alga was removed from Zone C. Note the clear sheath walls, healthy looking cells, and presence of hormogones.

of *Lyngbya* possessed thin colorless sheaths and lusterless yellowish cells with many vacuoles. The protoplasts were coarsely grained. Many hormogones were being produced. Amid the organic debris in zone D was a rich bacterial flora. (Fig. 5).

The lower-most zone E (4 to 10 mm below the surface) of the living algal mat community rests on or in a black, organic, silty, sandy sediment. The mat tends to merge directly with the physical and biological complex of these surface sediments when wet or covered with water. If the mat is exposed to air it dries and shrinks pulling away from the sediment. No light could be detected (Table 1) more than a millimeter into the band. The layer is reddish yellow due to the presence of both *Lyngbya confervoides* and an autotrophic purple bacterium. There are also many colorless flagellates and bacteria including *Beggiota sp.*, diatoms, and blue-green algae of the genus *Oscillatoria, Phormidium,* and *Schizothrix* (Fig. 6). The zone has an odor of hydrogen sulfide.

Growth of Filaments Under Conditions Simulating the Natural Zones

In Table 3 and Table 4 are summarized the results of the growth studies according to the zone. In each table is given the mean, standard deviation and the number of measurements of length of the trichomes.

Positive increase in weight (Table 3) was observed only in experiments simulating zones C and D, the same zones with the green appearance and thin sheaths. Apparently neither the surface conditions with the high light intensities nor the deep anaerobic conditions with little or no light were able to support net growth or the community dominant.

Positive increases in length of trichomes were also found in conditions of level C and D. In addition a few instances of increased length without increase in weight were found in conditions of zone E. Whether these cases involved heterotrophic nutrition, elongation without gravimetric gain, is not certain.

Of much interest is the positive growths in length and weight of filaments in conditions simulating zone D in the dark. It is possible that heterotrophic growth was taking place. It is possible that changes in salinity during transfer may have caused water uptake also.

Thus growth was observed in conditions simulating the lower intensities of the lighted zones and the layer immediately below the lighted zone.

Discussion of the Role of Each Layer

Each zone (A through E) in the algal mat profile appears to represent a habitat which differs with respect to trophic level from adjacent zones. Furthermore, additive growth appears to occur mostly in the central portion of the mat from zones B through the upper part of E.

Zone A

The role of the darkly stained surface layer in the community may be primarily that of a light and temperature shield for the sublayers of living organisms. Filaments under intense sunlight several millimeters deep within the mat crust are deeply stained. Therefore, as summer approaches the density of the pigment in the crust of the mat increases

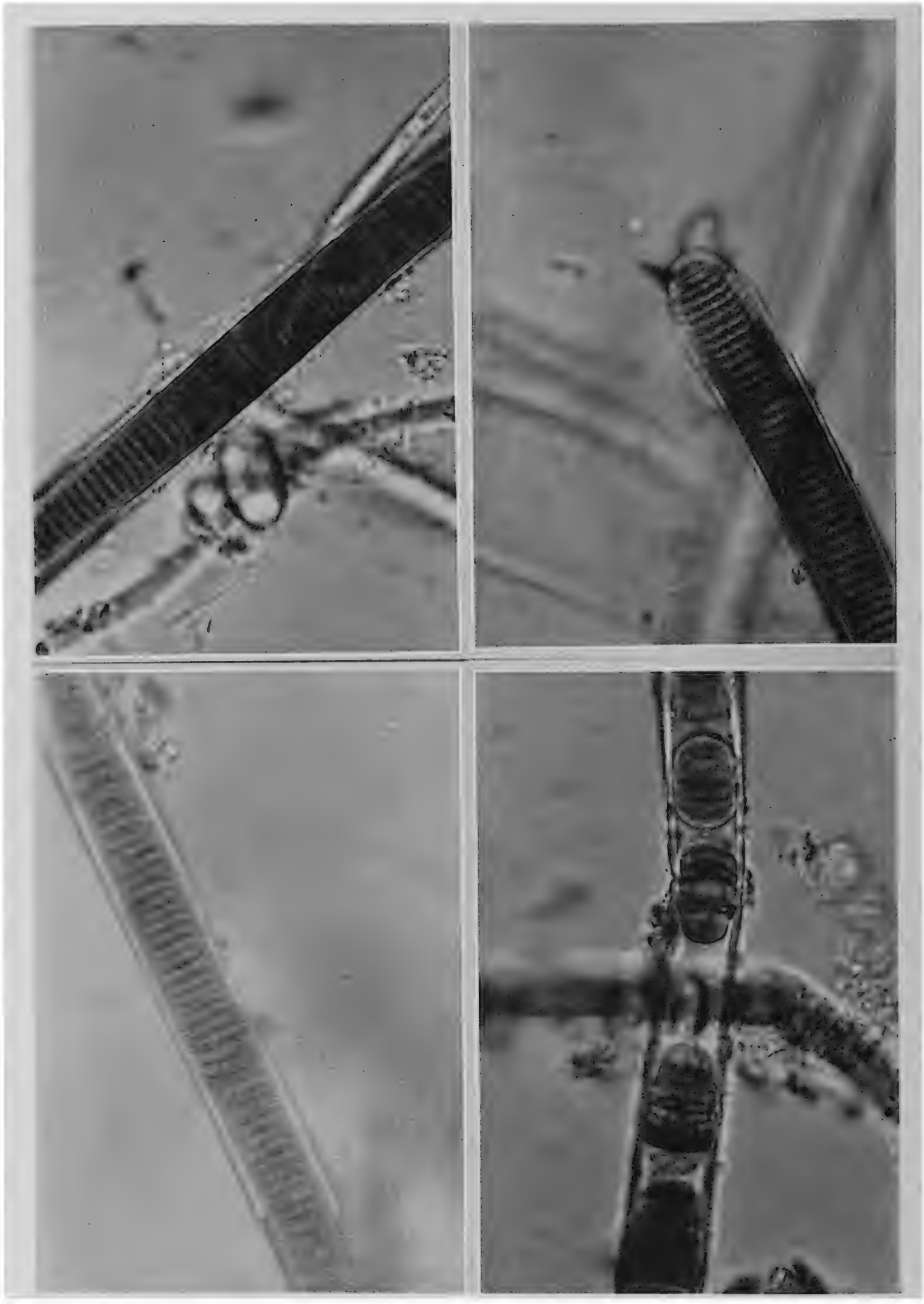

FIG. 5. Zone D. Photomicrographs of *Lyngbya confervoides* taken from Zone D, a yellow-tinted zone below the more lustrous blue-green band. Note the thin sheath walls, the presence of hormogones, and healthy appearance of the cells.

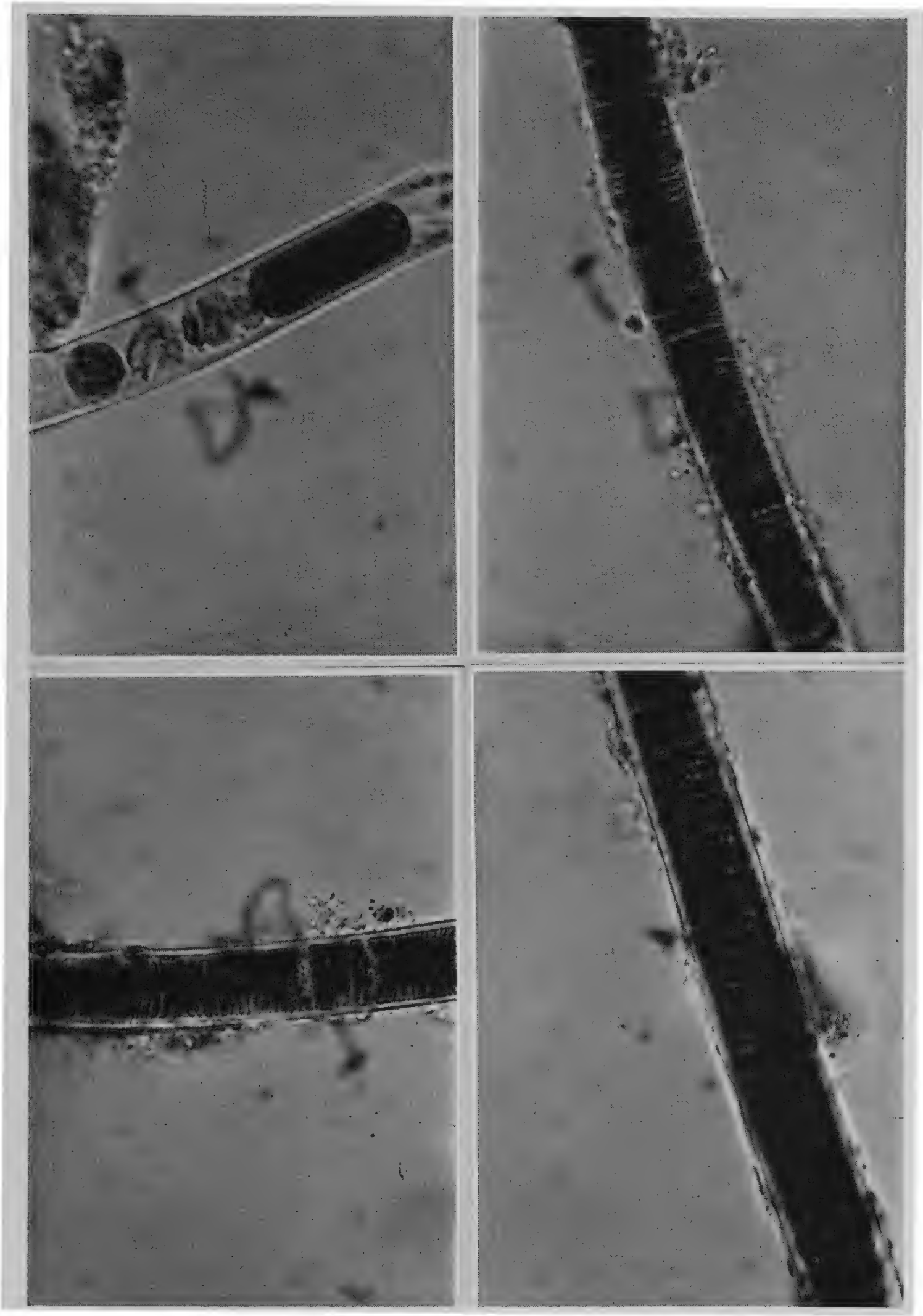

FIG. 6. Zone E. Photomicrographs of *Lyngbya confervoides* in Zone E near and at the bottom of the algal mat. Note the thin sheath walls, contraction of the protoplasts, balling-up of the cytoplasm, and presence of vacuoles.

TABLE 3

Gravimetric data for algal mat cultures of *Lyngbya confervoides* grown under conditions simulating the zones found in the natural algal mat (See Table 1)

Simulated zone	Beginning dry wt Mean	SD	N	Final dry wt Mean	SD	N	Growth rate in g/week* Mean	SD	N
A	1.3405	0.3962	12	1.2749	0.3819	12	—0.051	0.031	12
B	0.1781	0.0921	5	0.1658	0.0797	5	—0.047	0.111	5
C	0.8161	0.9383	8	0.9491	0.8589	8	0.72	0.70	8
D	0.0672	0.0172	12	0.1032	0.0122	12	0.62	0.43	12
E	0.107	0.025	16	0.083	0.014	16	—0.206	0.126	16

* Growth rate is based on a sample with an initial dry weight of 1 g. 4 sq cm of algal mat equals approximately 1 g. dry weight.
SD Standard Deviation.
N Number of measurements.

TABLE 4

Morphometric data for algal mat cultures of *Lyngbya confervoides* grown on microslides under conditions simulating those found in the natural algal mat (See Table 1)

Simulated zonal conditions	Initial length trichomes in mm Mean	SD	N	Final length trichomes Mean	SD	N	Per cent change in length Mean	SD	N
A	0.80	0.32	17	0.71	0.29	17	—11.0	6.3	17
B	0.82	0.24	8	0.81	0.22	8	—0.4	12.4	8
C	0.95	0.21	8	0.99	0.24	8	3.5	10.7	8
D	0.252	0.302	9	0.363	0.568	9	24.8	26.3	9
E	0.89	0.29	18	0.86	0.30	18	—2.9	9.7	18

SD Standard Deviation.
N Number of measurements.

and becomes more and more effective as a light shield. This conclusion was reached by the writers when they observed that nearly 95 per cent of the incident light (Table 1) is lost within the first 0.5 to 1.0 mm of the average algal mat crust.

The crust may suffer a general net loss, as suggested by the data in experiments on zone A (Table 3 and 4). In Fig. 7 a growth rate curve for the entire mat profile has been constructed upon data from the gravimetric experiments. In zone A of this postulated growth curve, the compensation point has been estimated to occur actually below the surface crust of the mat.

If there is a net loss in the surface layer, how is it possible for the crust to maintain itself? Patches of surface crust are often removed by high winds exposing the subsurface layers. Alternate drying and wetting of the mat tends to cause shrinkage and sloughing off of sections which may be floated or blown away. Yet, the surface layer appears to be renewed continually. Newly exposed mat surfaces will assume crustal characteristics. *Lyngbya* has motility which was often observed by the writers. The alga was also observed to have positive phototropism in moderate light (see Burkholder, 1934). Migration to the surface after dark and on overcast days would be possible. Hormogones likewise may help repopulate the surface by means of flotation. Results of an experiment (Table 5) indicated that in water containing 3 per cent salt or more the buoyancy of hormogones was positive. Pieces of mat or whole sections were observed floating on the surface of the water some seasons.

ZONE B

Some additive growth is probably contributed to the mat community from zone B beneath the light and heat shield of the surface crust. Data from experiments simulating

zone B (Tables 3 and 4) support this conclusion and the growth curve shown in Fig. 7 indicates the probable trophic relationship of this subsurface layer.

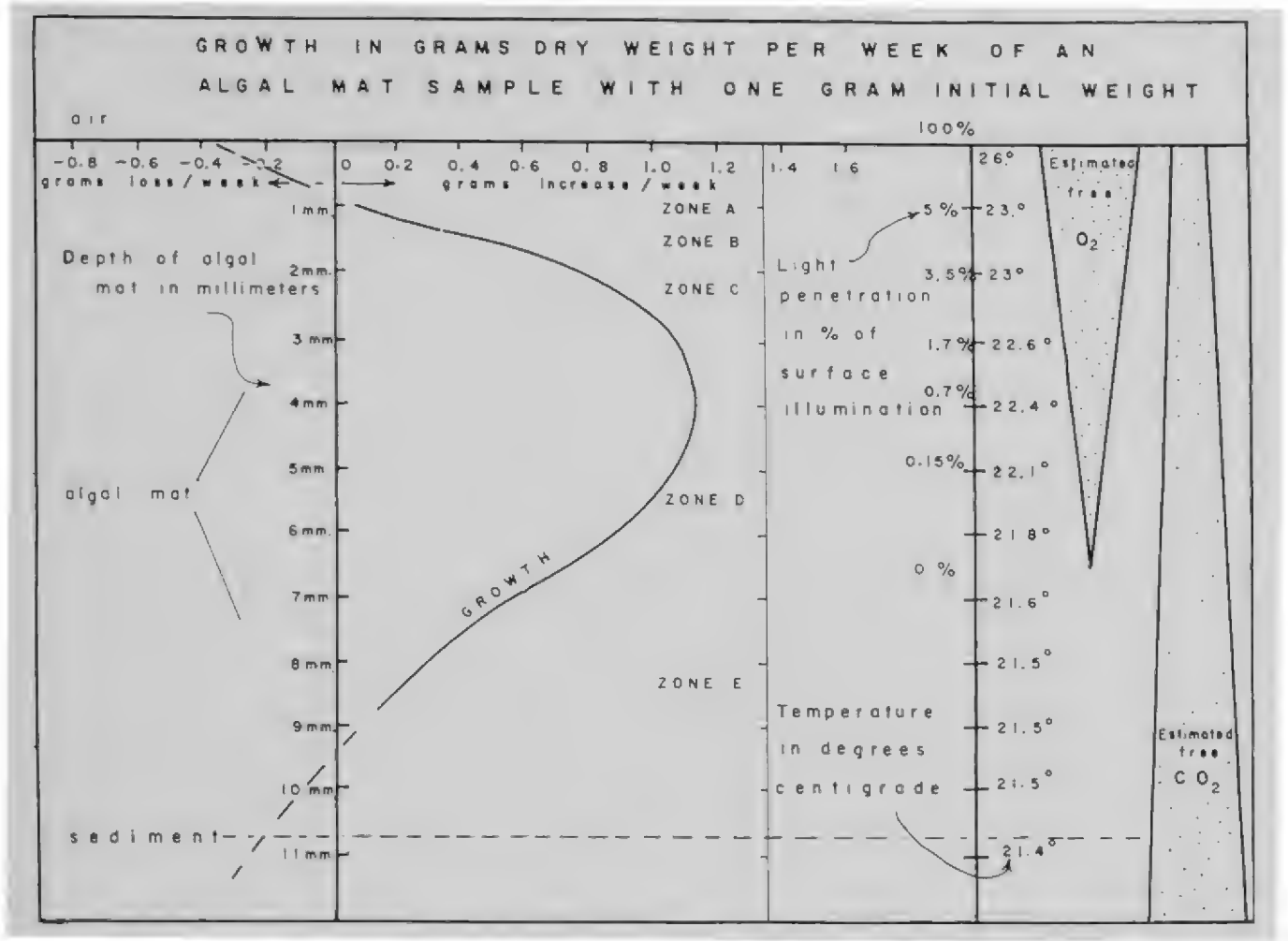

FIG. 7. Hypothesis of growth of *Lyngbya confervoides* within the mat profile based on experiments 1–5 estimated for the month of May. The growth curve also represents the general growth trend for the mat community since all mat organisms were contributing to the increases measured.

ZONE C

Experiments simulating zone C, data (Tables 3 and 4) and observations indicate that the mat community in the lustrous blue-green mid-layer is growing vigorously. Additive growth is probably greatest in this zone. The amount of light penetrating into this zone is apparently more than enough (Table 1) to sustain and provide storage products in plant life. This alga and others may also be utilizing organic substances. Bacteria increased in importance from zone C downward as shown by the increasing numbers observed in samples from these zones under the phase microscope.

ZONE D

Results from experiments simulating zone D (Tables 3 and 4) infer that additive growth takes place in this zone. However, the zone is a marginal habitat in which intensities above the compensation point are apparently seldom reached. This situation may involve a facultative heterotrophic plant community, cell migrations, transport of materials and other possible mechanisms.

ZONE E, HORMOGONES

Zone E is apparently a zone of decomposition, anaerobic processes, and consumers ultimately dependent on the photosynthetic activity above. Material from this zone may

be one of the sources of organic matter in lagoonal paleoenvironments. The hormogones produced here are capable of emerging to the surface due to their buoyancy, this aiding in transport and dispersion of the dominant species (Table 5).

TABLE 5

Data for the buoyancy of hormogones, trichome-filled and empty filaments of *Lyngba confervoides* from living material obtained from Zone C of an algal mat community. A plus sign indicates positive and a negative sign negative buoyancy

Medium	Hormogones		Living filaments		Empty sheaths	
	+	—	+	—	+	—
FRESH WATER	0	23	3	18	3	22
SALT WATER (30‰)	12	1	1	10	0	16
BRINE (200‰)	16	0	1	21	2	29

Acknowledgments

Grateful acknowledgment is given to Mr. R. Lamplugh, technical assistant, and to Dr. Louis S. Kornicker and Dr. Carl H. Oppenheimer for valuable suggestions. Dr. Harold Humm kindly confirmed the identification of *Lyngbya confervoides*. Photographs of the habit of the algal mats (Fig. 1) were kindly provided by Dr. Kornicker. The study was supported in part by the University of Texas and Pan American College, Edinburg, Texas.

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Zinc in a Texas Bay[1]

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Abstract

Using a dithizone method for organisms and sediment and a lanthanum precipitation for sea water, concentrations of zinc were determined in the water (8, 15 ppb), sediments (10–18 ppm), underwater plants (60–100 ppm), and animals (9–130 ppm) predominating in the grass flats of Redfish Bay, a shallow marine estuary near Port Aransas, Texas. Values of zinc concentration were multiplied by estimates of dry weight of the principal components per square meter to obtain a zinc inventory of the grass flat. Over 300 mg/m^2 was found in the underwater plant components; 300 mg/m^2 in each centimeter of sediment; and less than 0.4 mg/m^2 in the animals.

Introduction

Zinc is of biological importance in the sea. Several papers have been cited by Malmstrom (1956) which review the metabolic importance of zinc. Bachmann and Odum (1960) have shown that the rate of uptake of radioactive zinc-65 from sea water was proportional to the gross oxygen production for six species of marine benthic algae. Rapid uptake of zinc-65 by marine plankton and shellfish has also been reported (Chipman, Rice and Price, 1958). The fact that many marine organisms geatly concentrate zinc over the concentration found in sea water is probably a reflection of the biological importance of zinc.

It is known that sea water is deficient in zinc. There is very much less zinc in sea water than would be expected from an estimate of the amount of zinc supplied to the oceans due to the weathering of rocks (Rankama and Sahama, 1950). Krauskopf (1956) has shown that sea water is undersaturated with respect to any insoluble compounds of zinc that might form from the ions normally present in aerated sea water. He suggests that local precipitation of sulfides might control the concentration of zinc in sea water.

That zinc is biologically important and present in sea water in only trace amounts leads one to wonder whether it may be important in determining the amount and type of life present in a bay. This paper contains the early results of a study of the chemistry of zinc in a shallow bay dominated by turtle grass beds. The concentration of zinc in the various phases of a bay (sediment, water and organisms) was determined colorimetrically. Attention was given to modifying and developing suitable chemical techniques. A new method for the isolation of zinc from sea water prior to its determination is given.

This research was a continuation of work under AEC Contract No. AT(40–1) 2580 begun earlier by Dick Hunter and H. T. Odum.

[1] Supported by the United States Atomic Energy Commission through Contract No. AT(40–1)2580.
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Experimental Methods

Zinc in biological materials was determined by the method of Sandell (1959). The sample was decomposed by ashing in a porcelain crucible at 450°C. The ash was taken up in 4 N HCl, and insoluble material removed by filtration. A preliminary separation of zinc was effected by making this filtrate basic with ammonia, adding citrate to hold back iron, and extracting zinc with a 0.01 per cent solution of dithizone in carbontetrachloride. The extraction was repeated until the organic layer remained green. The zinc was stripped from the carbontetrachloride with two 10 ml portions of 0.02 N HCl. This solution was made up to volume. A ten ml aliquot of this solution was treated with five ml of an acetate buffer (pH 4.75) and one ml of a 25 per cent sodium thiosulfate solution. This solution was shaken with 10 ml of a 0.001 per cent dithizone-carbontetrachloride solution. The optical density of the organic phase was measured versus a dithizone-carbontetrachloride solution at 530 millimicrons. The concentration of zinc was read from a standard curve previously prepared by the same method. Sediment samples were treated in the same way after they were first decomposed with an HCl-HNO_3 mixture. This procedure was found to give satisfactory results for samples of organisms and sediment both of which were highly enriched in zinc compared to sea water. Analytical error was less than 20 per cent of the value given. For the determination of zinc in sea water a new method for the isolation and purification prior to the final dithizone determination was needed.

Iron hydroxide will remove zinc from sea water, but the iron thus introduced interferes with the later determination of zinc. The removal of zinc from sea water by the precipitation of lanthanum hydroxide was investigated by use of the radioactive isotope zinc-65. After a known activity of tracer has been added to 500 ml of filtered (Whatman No. 40) sea water, 50 mg of lanthanum as the chloride was added. The hydroxide will form at the pH of sea water. However, a few drops of ammonia were added until the pH was just below 9. The lanthanum hydroxide was collected on Whatman No. 41H filter paper, and then was removed by dissolving it in 25 ml of 4 N HCl. A lanthanum chloride blank was found to contain no zinc within the limits of detection.

The HCl solution containing the lanthanum and zinc must be purified by a method other than the basic dithizone extraction used on the biological samples because the hydroxide will reappear if the solution is made basic. Kraus and Moore (1953) have studied the behavior of zinc in HCl on the anion exchange resin Dowex-1. They report that zinc is very strongly adsorbed. This behavior has been used by Rush and Yoe (1954) in connection with the Zincon reagent and modified by Maier and Bullock (1958). In the present work the 4 N HCl solution was passed through a 7×0.5 cm column of Dowex-1-X 8, 50–100 mesh in the chloride form. Zinc and a few other metals were adsorbed on the resin. The column was then eluted with 25 ml of 0.5 N HCl. This removed iron and the other transition metals, but left zinc and cadmium. Zinc was then eluted with 25 ml of 0.005 N HCl at a flow rate of 0.5 ml per min. This 0.005 N solution was then used in the dithizone determination method already described. A correction for chemical yield was made on the basis of the zinc-65 recovered. A blank showed the resin could be washed free of zinc with 0.005 N HCl. Table 1 has the results of a radio-chemical study of the procedure outlined here.

Lanthanum hydroxide is a very useful collector for trace elements in sea water. It is

TABLE 1

Distribution of zinc-65 in the isolation and purification procedure

Fraction	Zn-65 recovery percent*
First $La(OH)_3$	80
Second $La(OH)_3$	10
Sea water after two lanthanum precipitations	2
Stuck to the glassware and removed by strong HCl	5
Eluted from Dowex-1 (based on amount put on column)	100
Typical recovery for whole procedure	91

* The counting error is less than 2 percent.

being used as a collector for manganese as well as for zinc. It is available in high purity, and it can be easily removed from the trace metal as in the case of zinc by ion exchange.

Results and Discussion

Samples collected from turtle grass beds of Redfish Bay located near the Institute of Marine Science were analyzed for their zinc content using the methods described. Results for the biological samples are reported on a dry weight (110°C) basis. These results are given in Table 2. The values found for the zinc content of the bay water are in

TABLE 2

Results of zinc analyses

Sample	Description	Zn ppm*
Bay water	salinity 34.4‰, Aug. 18, 1960	0.008
Bay water	salinity 14‰, Dec. 8, 1960	0.006
Sediment	upper 15 cm	10 to 18
Algae	*Digenia simplex*	60
Algae	*Gracilaria sp.*	89
Turtle grass	*Thalassia testudinum*	100
Thin grass	*Diplanthera wrightii*	88
Mullet	*Mugil cephalus*	130
Pinfish	*Lagodon rhomboides*	113
Silverside	*Menidia sp.*	51
Killifish	*Fundulus similis*	29
Croaker	*Micropogon sp.*	43
Brown shrimp	*Penaeus aztecus*	45
Grass shrimp	*Palemonetes sp.*	70
Blue crab	*Callinectes sapidus*	46
Clam	*Chione cancellata*	9
Clam	*Lucinia floridana*	25
Barnacle	*Balanus eburneus*	36

* Average of 3 or more analyses each.

the range for normal sea water (Harvey, 1957). The zinc values for sediment samples are in the lower end of the range of those reported by Ishibashi (Ishibashi, Ueda and Yamamoto, 1959) for a shallow bay in Japan. All of the biological samples analyzed have concentrated zinc several thousands over the concentration in sea water. The organisms thus far analyzed (Table 2) represent a small fraction of the total number of species which live in the bay. However, due to the predominance of turtle grass, *Diplanthera*, and the animal species studies, (Hellier, 1962), they contain much of the zinc which is held in the bay system.

The values reported in Table 2 have been multiplied by the absolute abundance (standing crop dry weight) of each component listed to calculate a zinc inventory for the bay. The abundance values for the animals were taken from a study by Hellier (1961). The abundance values for the grasses were measured in the same grass flat from which the samples were collected. The results of these calculations are presented in Table 3.

TABLE 3

Zinc inventory for a grass flat

Sample	Description	Dry weight g/m^2	Zinc content mg/m^2
Bay water 34.4‰	lm depth	10^6	8.0
Sediment	per cm depth	10^4	300
Turtle grass	summer crop	3000	300
Thin grass	summer crop	568	50
Mullet	max biomass	2.3	0.3
	min biomass	0.061	0.008
	avg biomass	0.61	0.08
Pinfish	avg biomass	0.18	0.02
Blue crab	max biomass	1.5	0.07
	min biomass	0.065	0.003
Brown shrimp	max biomass	0.067	0.003

This type calculation clearly indicates that a huge reservoir of zinc was held in the top few cm of the sediment. As long as an effective mechanism is available to return some of this to the cycle, the life in the bay can never suffer from a zinc shortage. How this recycling is accomplished is not known. The organisms with the highest zinc inventory are also the ones most intimately associated with sediment, suggesting direct removal from the sediment by these organisms or a utilization of zinc which has been accumulated by the microorganisms living in the sediment.

The inventory in Table 3 is an idealized one intended to show the general pattern of zinc distribution. Actually, all the materials listed may never be present in the same square meter.

Although the two series of bay water samples contained different amounts of zinc, both values were small compared to other items in Table 2. The analytical error was at most 25% and not enough to account for the difference between 8 ppb and 15 ppb. The higher value was from water of low salinity (14‰).

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The Microbial Decomposition of Organic Carbon in Surface Sediments of Marine Bays of the Central Texas Gulf Coast[1]

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Abstract

Studies were made of 28 sediment profiles over a period of eight months in a shallow marine lagoon, Redfish Bay, near Aransas Pass, Texas.

Organic carbon, bacterial populations, forty-day rates of organic carbon decomposition, sediment grain size and texture were measured in the cores from five stations. Organic matter (as low as 0.1%) was minimal in winter and more refractory than in fall or spring. Bacterial counts (2.0 to 200×10^6) and organic matter (3.7%) were highest in coarse surface sediments near shore in summer possibly correlated with photosynthetic algal production. Organic matter below the surface was less concentrated and refractory. Considerable decomposition was observed in samples kept at 4° C. In shore zones rods and cocci in fall and winter were replaced with other types in summer.

Introduction

Microorganisms occupy an important position in the ecology of a marine environment. The total organic matter, whether dissolved, particulate, or bound in protoplasm, must be continually mineralized for life to continue. Bacteria are primarily responsible for the decomposition of organic compounds synthesized by plants and animals to simple compounds and elements. Odum and Hoskin (1958) estimate the average annual primary production of organic matter by plants in the shallow bays of Texas near the Institute of Marine Science, 5 g per square meter of bay surface per day. Bacteria also contribute to organic matter by the synthesis of bacterial cell substances during growth. ZoBell and Feltham (1938) estimate that several milligrams of bacterial organic matter is produced per day per top 5 cm of a square meter of mud in a shallow marine mudflat.

The total bacterial population of a marine environment is difficult to determine. Both direct microscopic analyses and standard plate count methods have serious limitations (Jannasch and Jones, 1959). Direct microscopic examination is limited because of the problem of distinguishing between particulate matter and bacteria. Plating procedures are inaccurate because the type of medium, temperature, and duration of incubation are selective for restricted groups of organisms. Because no reliable procedures are available to measure total bacterial numbers, Emery and Rittenburg (1952) suggest that bacterial activity may be estimated by a study of the time changes of materials known to be affected by microbial activities, such as total organic carbon.

In the following study the rates of microbial activities in the sediments of highly pro-

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ductive shallow marine bays of the Texas coast were measured by an indirect method involving the study of the changes in total organic matter. Seasonal variations, lateral variation, vertical variation, and effect of the types of sediments can be estimated. One must assume, however, that the changes in the content of organic matter are directly related to the activities of microorganisms. Where large burrowing organisms are not abundant, it may be assumed that the net organic matter in the sediment will not be changed much by the activities of the larger invertebrates. The following data are derived from approximately 8 months of research in 1958 and 1959 on the changes of organic matter and microorganisms in Red Fish Bay, Texas (Fig. 1.).

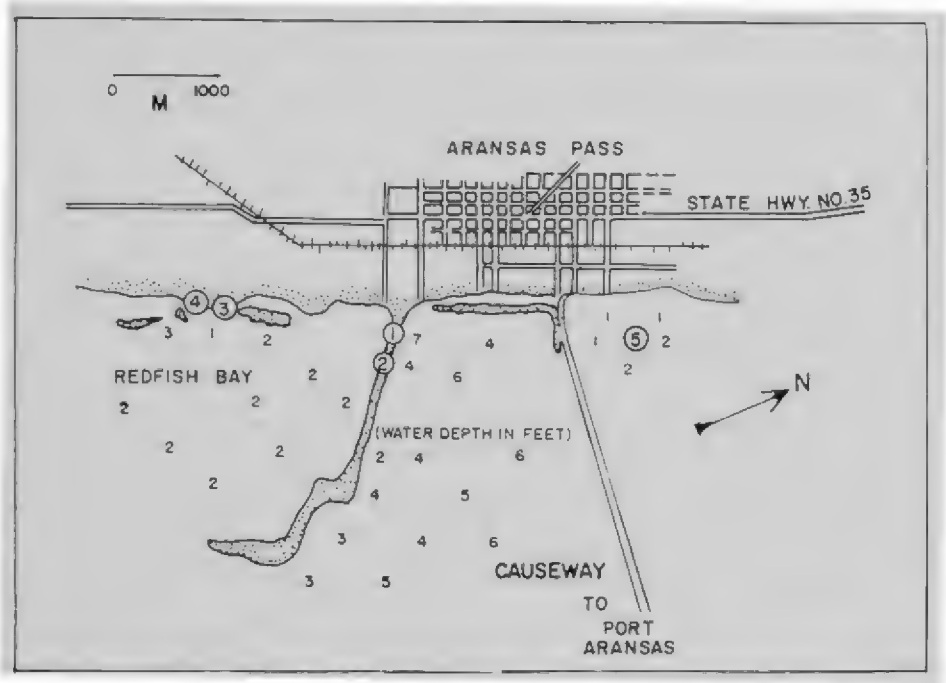

FIG. 1. Approximate locations of five field stations in Redfish Bay.

History

The total amount of organic matter in marine sediments has, in the past, been determined by four methods, each procedure having inherent errors (a recent survey of carbon procedures is given by Duursma, 1961):

1. *Ignition of sample* and determination of loss in weight. The ignition method is not selective for organic matter because calcium carbonate and other volatile inorganic materials may be included. Trask (1939) has shown that fine clays lose more water than sandy material, causing error in ignition studies.

2. *Determination of a reduction number.* The method of Schollenberger (1927) for the determination of the reduction of chromic acid by sediment has been modified by Trask (1939). The amount of reduction has been considered an index of total organic content. However, the type and state of oxidation-reduction of the organic material in the sediments will affect the amount of chromic acid which can be reduced.

3. *Extraction of organic matter.* The amount of time needed for extraction limits its usefulness. Also, most solvents are not capable of removing all the organic matter.

4. *Determination of organic carbon by wet combustion.* The determination of organic carbon and the use of a conversion factor of 2 to convert carbon to organic matter was first suggested by Boysen-Jensen (1914). Waksman (1933) suggested a factor of 1.887, and Trask (1932) proposed using a factor of 1.7 for marine sediments. In comparing the total organic matter with the organic carbon values of the same sediment

samples, Bader (1954) found that conversion factors varied from 1.49 to 2.5. Therefore, Bader suggested that organic carbon values *per se* be reported.

Much of the information on the distribution of organic matter in ancient and recent marine and estuarine bottom deposits has been published by Trask (1932, 1939), who reported that the amount of organic carbon in sediment may be inversely related to particle size. Krumbein and Caldwell (1939), Emery and Rittenberg (1952), and Bader (1954) have also observed in recent and older sediments that the organic carbon increases with decreasing grain size. In their studies of Central Texas Gulf coast sedimentation, Shepard and Moore (1955) found no direct correlation between percentage of carbon and percentage of clay.

Organic carbon is normally found to decrease with an increase in sample depth from mud surface (Trask, 1932, 1939; Krumbein and Caldwell, 1939). Shepard and Moore (1955) and Murray (1956), however, find no marked variation in carbon with depth of sediments, and often a slight increase in organic carbon with increased depth is observed.

The effects of sample depth and type of sediment on bacterial population in sediments have been studied by Emery and Rittenberg (1952). They indicate that the upper layers of sediments usually contain larger bacterial populations. However, occasionally subsurface samples give higher counts than surface samples. A larger bacterial population in a subsurface sample appears to be correlated with an abrupt increase in water content and decrease in cohesiveness. Reuszer (1933) stated that the distribution of bacteria is related directly to the organic content of the sedimentary layers. The higher organic content of clays and silts is perhaps responsible for the greater abundance of bacteria often associated with the finer sediments. ZoBell (1943) found that bacterial multiplication and survival were enhanced by solid surfaces. The small clay and silt particles (1–2 microns), with more surface area, support a larger bacterial population than coarse sands (Wood, 1953). Oppenheimer (1960) gave an account of bacterial activities of sediments of shallow marine bays.

In half of the sediment cores analyzed by Anderson (1939), the surface carbon was decomposed easily and the rate of decomposition decreased gradually with depth. In other cores, organic matter which was buried in anaerobic conditions, was much more easily decomposed. Thus the amount of organic matter available to bacteria varied within the sediment profile. Microbial decomposition of organic matter was not always greatest in the surface layers. Usually, a small fraction of buried organic matter is resistant to microbial decomposition. The refractory material (humus) is composed primarily of a ligno-protein complex and a hemicellulose-protein complex (Waksman, 1933).

The decomposition coefficient (degree of decomposition of total organic matter) was compared by Bader (1954) with the density of pelecypods in sediments. An extraction method was used to measure non-refractory organic matter. Pelecypod numbers were found to increase when the per cent of non-refractory organic matter increased. Thus, the amount of available organic matter may be significant to the support of populations of organisms which utilize the particulate organic matter in sediments.

Methods

Collection Areas

Red Fish Bay, partially shown in Fig. 1, is a shallow marine bay of the Central Texas

Gulf Coast, having an average water depth of 0.6 m and a high degree of plant productivity. Daily and semi-daily tides have little amplitude, less than 15 cm. The effective tides in the Bay are more dependent upon wind direction, and the tidal influence may have a duration of one to several days. Seasonal differences in sea level create higher water levels in the spring and autumn months. Little fresh water enters the Bay, and the nearest source of Gulf sea water is from Aransas Pass through the Barrier Islands, approximately 8 miles distant. The salinity may vary from 7 to 28 ‰ depending on rainfall. The mean monthly temperatures are difficult to evaluate because of the large variation. For example, in January 1958 the average temperature was 14°C, while the minimum-maximum was 7–23.3°C. The April average was 23.3°C and the minimum-maximum was 14.5–33°C. Spring usually occurs in March or late February. Four field stations (Fig. 1) were selected on the shores of Red Fish Bay and marked by metal stakes. Those stations were alternately dry or covered by water during wind driven tides. An additional station (No. 5) was located in an area in the Bay covered by approximately 50 to 75 cm of water depending on wind.

The area 1 marked by stake 1 was predominately a clay environment. The beach had a gentle slope, and the quiet water allowed the finer suspended material to settle out. Sea grass layers and alternating oxidized or reduced zones were found in the sediment profiles of this field station. Station 2 was located in an area of coarser sediments where water movement was greater. The profile of station 2 was more homogeneous, and no sea grass fractions or zones of reduction were observed. Abrupt changes in the texture of the sediment were often noted in the profile. Alternating layers of sand, shell, and spotty areas of ferric hydroxide deposition were noticed.

At station 3 clay minerals predominated in the subsurface sediments, while the surface layers had a coarser composition. The sediments were highly compacted, and profiles contained buried sea grass layers and distinct oxidized or reduced zones. Station 4 had a high shell content, which often comprised 75% of the sample.

Sediments of the bay station 5 were predominately clay with several sea grass layers in a profile. The sediments were usually reduced below 2 cm and hydrogen sulfide gas was detectable.

Directions for Locating Stations

A road log for field stations 1 and 2 starts in Aransas Pass at the intersection of state Highway 35 and Farm Road 632. Farm Road 632 (South Commercial Street) is followed for 0.9 mile to the intersection with Ransom Drive. The road log continues east on Ransom Drive for 0.55 mile. Field station 1 is located 126 yards from Ransom Drive on the Bay shoreline. Stake 2 is placed 235 yards east of Stake 1.

A road log for stations 3 and 4 starts in Aransas Pass at the intersection of State Highway 35 and Farm Road 632. South Commercial Street (Farm Road 632) is followed for 1.7 miles to the intersection with East Beasely Street. The road log continues east along Beasely Street for 0.95 mile. Stake 3 is approximately 0.15 mile southwest from the road. Stake 4 is 76 yards southwest of stake 3.

The bay station 5 is 1.25 miles north from the causeway and 0.4 mile east of the mainland shore.

Collection of Samples

A wedge-shaped portion of sediment was removed from each shore station, bisected lengthwise, and distinct sedimentary layers were transferred to sterile sample jars and transported to the laboratory. Areas selected included aerobic, anaerobic, sand, shell, clay of various mixtures, and layers of decaying sea grass. The depth of the sedimentary layers was recorded. Samples were not collected from sediment depths exceeding 20 cm.

Samples were collected from station 1 and 2 on the same day, while the next day stations 3 and 4 were sampled.

The bay sediments were collected in a plastic tube which was pushed into the sediment. The plastic tube was then filled with water, the top of the tube stoppered, and the water and sediment filled tube withdrawn from the sediment. A rubber stopper was placed in the bottom of the tube, and the column of sediment was forced to the top of the tube. Sedimentary layers were removed to sample jars.

Preservation of Samples

Sediment samples were refrigerated at 4°C except for short intervals when aliquots were removed for the analyses. Carbon was determined within four hours after collection. After 40 days incubation at 4° C the carbon was redetermined. The anaerobic sediments did not remain in the anaerobic state because of the storage conditions and the necessity for thorough mixing of the total sediment before aliquots were removed for analysis.

Aerobic Bacterial Plate Counts

One gram aliquots of the sediments were removed from the sample jars before refrigeration and transferred to 75% sea water dilution blanks. The highest dilution used for plating was 1:1,000,000. ZoBell's medium 2216 plus 1.5% agar (ZoBell, 1946) was used for estimating the aerobic bacterial population of the sediments. Two dilutions were plated in duplicate, and the plates incubated for a week at 23°C.

Microscopic Examination

Slides were prepared by mixing a few milligrams of sediment with a drop of sea water. A cover slip was then touched to the edge of the drop, permitting a flow of liquid under the cover slip by capillary action. Five fields were examined by phase contrast microscope and the variety of microorganisms tabulated for each sedimentary layer.

Water Content

The sediments collected in the sample jars were mixed thoroughly. An aliquot between 1 and 5 grams was removed and transferred to a tared porcelain crucible, and the sediment weight determined with an analytical balance. The crucibles were heated at 100°C for 18 hours, removed from the oven, cooled in a dessicator, and reweighed to determine water content. Duplicate analyses were made. All carbon values are % dry weight.

Organic Carbon Determination

The organic carbon content of the sediments was determined by wet combustion using Corcoran's (1957) modification of the Krogh apparatus (Fig. 2).

The sediment to be analyzed was thoroughly mixed in the sample jar. A weighed sample, containing between 1 and 10 milligrams of organic carbon was transferred to reaction flask (A). Two and one half ml of 50% phosphoric acid was added to the combustion vessel to convert carbonate carbon to carbon dioxide, which was then flushed from the train by a stream of oxygen. After 20 minutes all the carbonates were removed.

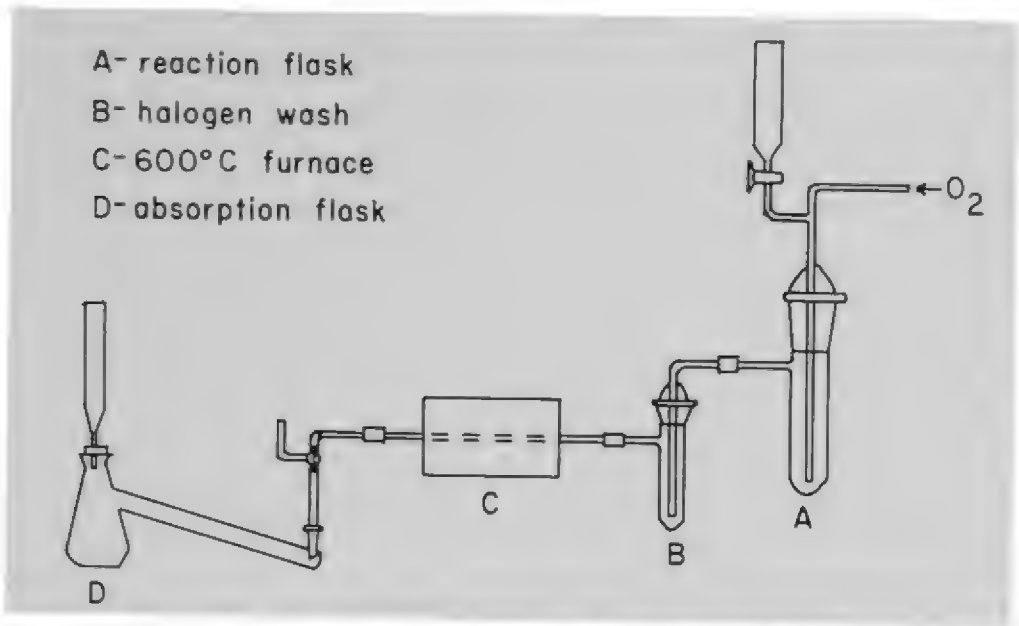

FIG. 2. Micro apparatus for measuring organic carbon in sediments.

The oxygen supply was cut off, and 5 ml of the oxidizing agent was added to the sediment from a reservoir attached to the top of the reaction flask. The oxidizing agent was a mixture of 16 g potassium dichromate, 48 g of silver dichromate, and 500 ml of concentrated sulfuric acid. The system was again slowly flushed with oxygen, and the reaction vessel heated at a constant temperature of 50°C for 30 minutes. The oxygen carrying the carbon dioxide and monoxide passed through the halogen wash (B), copper oxide catalyst (600°C) (C), and was slowly bubbled through 10 ml of the baryta solution in the receiving arm of the absorption flask (D). Flask (B) contained 5 ml of a halogen wash, composed of 20 g of potassium iodide, 50 ml of 10% sulfuric acid, and 1 g of powdered antimony. The halogen wash was employed to trap any escaping chlorine as antimony chloride. Any carbon monoxide from incomplete combusion was converted to carbon dioxide by the copper oxide catalyst at 600°C. The baryta solution was a mixture of 1 part saturated barium nitrate solution and 2 parts saturated barium hydroxide solution, diluted to 0.1N.

At the end of the combustion period the absorption flask was removed from the train, and the excess barium hydroxide titrated with 0.1N hydrochloric acid. The difference in the titer between the original baryta solution and the final solution was proportional to the amount of organic carbon contained in the seliment sample.

With this method 1–10 mg of organic carbon can be measured with an approximate error of 1%. Corrections were made for water content of the sediments, and the organic carbon reported on a dry sediment basis.

The organic carbon was redetermined after 40 days storage at 4°C. A 40 day storage period permitted an almost complete decomposition of organic matter. At the end of 40 days bacterial activity had either ceased or proceeded at a very decreased rate. Refrigeration at 4°C closely simulated the environmental conditions found in the sediments during the winter period. The loss in carbon after the 40 days storage at 4°C was assumed to be proportional to the amount of bacterial activity in the sediments.

GRAIN SIZE ANALYSIS

Grain size was estimated with 5 sieves of standard Tyler screen sizes. Originally designed for field use, the apparatus consisted of 5 screens, 1 inch in diameter, mounted in a plastic tube and arranged 2 inches apart in descending order of pore size. The dis-

tance between the screens was marked by 20 equal divisions etched on the plastic tube. An aliquot of sediment was measured in a calibrated plastic cup and transferred to the upper screen. The apparatus was constantly agitated and sea water added to facilitate division of the sample into the component grain sizes. The per cent of different sized particles in a sample could be estimated by comparing the levels of the material collected on the various sieves with the lines etched on the plastic tube. The silt and clay fractions of the sediments were not retained by the sieves. The material collected on the first two screens was composed of shells, shell fragments and sea grass.

The sieves used had the following Tyler screen sizes: 1, greater than 1 mm; 2, coarse sands with diameters between 0.5 and 1 mm; 3, sands with diameters between 0.25 and 0.5 mm; 4, fine sands with diameters between 0.125 and 0.25 mm; and 5, very fine sands with diameters between 0.062 and 0.125 mm.

Results

Twenty-eight sediment profiles are presented histographically and grouped according to station in Fig. 3 to 10. The four histograms on each sediment profile represent the same sample, and each bar denotes a sedimentary layer. The top bar is the surface layer of the profile, and the depth in millimeters for the other sedimentary layers is placed opposite the appropriate bar. The results of a preliminary survey of the sedimentary environments along the shores of Red Fish Bay are presented in Fig. 3. Bacterial counts are not recorded for these samples.

The seasonal change in organic carbon is presented in Figure 11. Two field stations 1 and 2 (Fig. 4–7) have been sampled monthly from October through April to include both a clay-sand and sand-clay environment in the seasonal study. The average initial carbon and carbon after 40 days storage is graphed for the two field stations.

The types of bacteria found in the shore sediments (stations 1–4) show a slight change with the seasons, whereas those in the Bay at station 5 (Fig. 11) had no apparent change. At stations 1, 2, 3, and 4 rods were predominant in October; rods and cocci November through February; and spirilla, rods, diplococci, and cocci in March and April. At bay station 5 spirilla, rods, diplococci, cocci, and vibrio were predominant October through April. Seasonal variations in counts of bacteria are presented in Table 1.

TABLE 1

Minimum bacterial populations in sediments from Redfish Bay, Texas, as determined by standard plate count procedure. Millions per gram of wet sediment.

Month	Area 1		Area 2	
	Surface	1 cm	Surface	1 cm
October			5.7	1.5
November	0.5	0.2	9.6	....
December	2.7	1.7	8.4	19.0
January	1.8	1.0	5.5	4.2
February	5.4	8.0	6.5	1.3
March	25.0	49.0	16.0	1.7
April	55.0	7.5	49.0	9.0
June	140.0	70.0	....	....
July	100.0	2.0	70.0	100.0
August	150.0	10.0	200.0	1.0

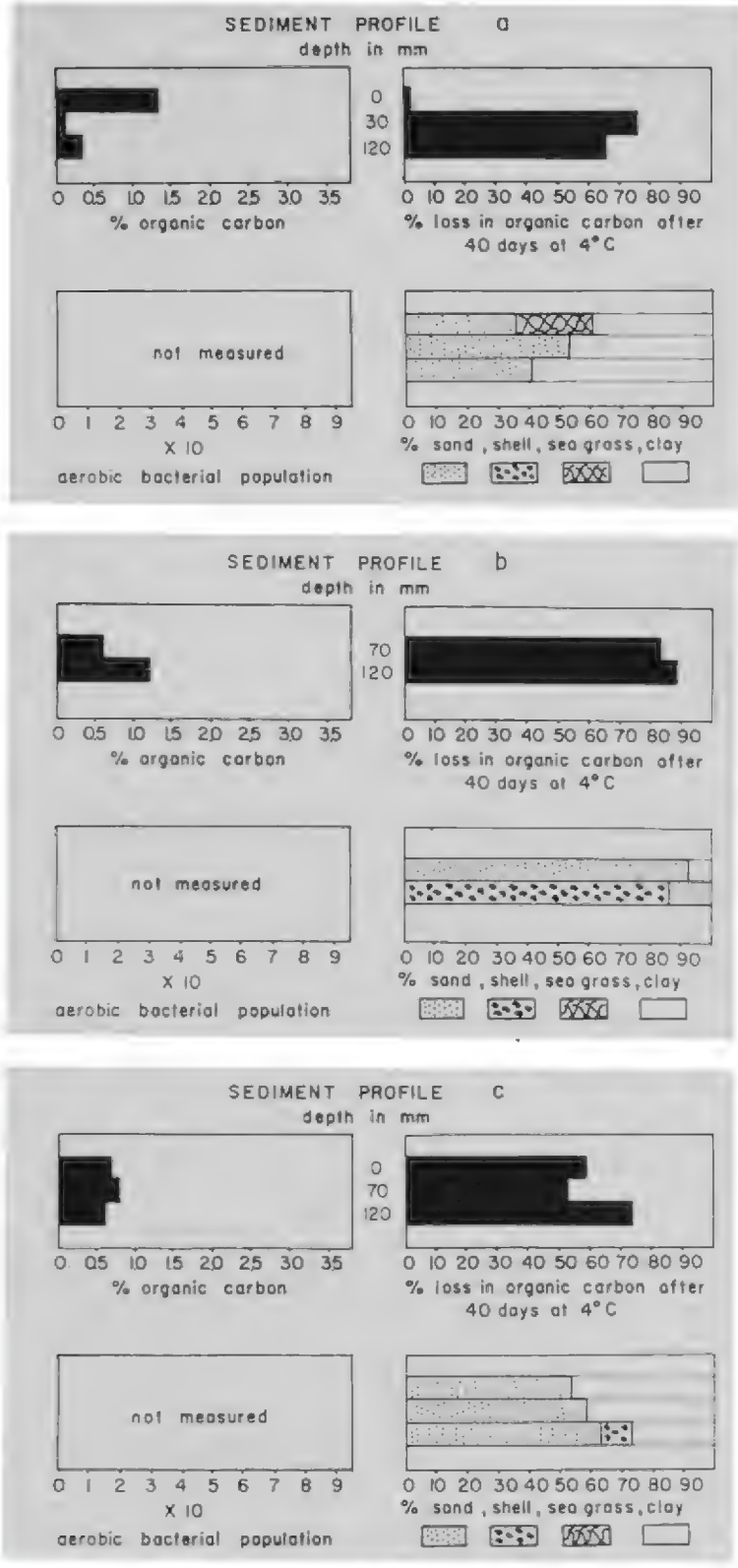
SEDIMENT PROFILE a
depth in mm
0
30
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
not measured
0 1 2 3 4 5 6 7 8 9
X 10
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
70
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
not measured
0 1 2 3 4 5 6 7 8 9
X 10
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0
70
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
not measured
0 1 2 3 4 5 6 7 8 9
X 10
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 3. Analysis of sediments during preliminary survey October 1958. Surface sediments collected between areas 1 and 2.

Discussion

Monthly profile samples of the shoreline sediments in Red Fish Bay collected from single stations show considerable differences in texture and placement of oxidized and reduced zones. The variations in sediments within short lateral and vertical distances make it difficult to compare the data obtained. However, the uneven sediment distribution is significant for understanding microbial activities in sediments and the subsequent diagenetic processes taking place. Our data indicate that microbial activities are related to the available organic matter. The uneven distribution of the organic matter may thus be a primary factor in the formation of varied microfacies.

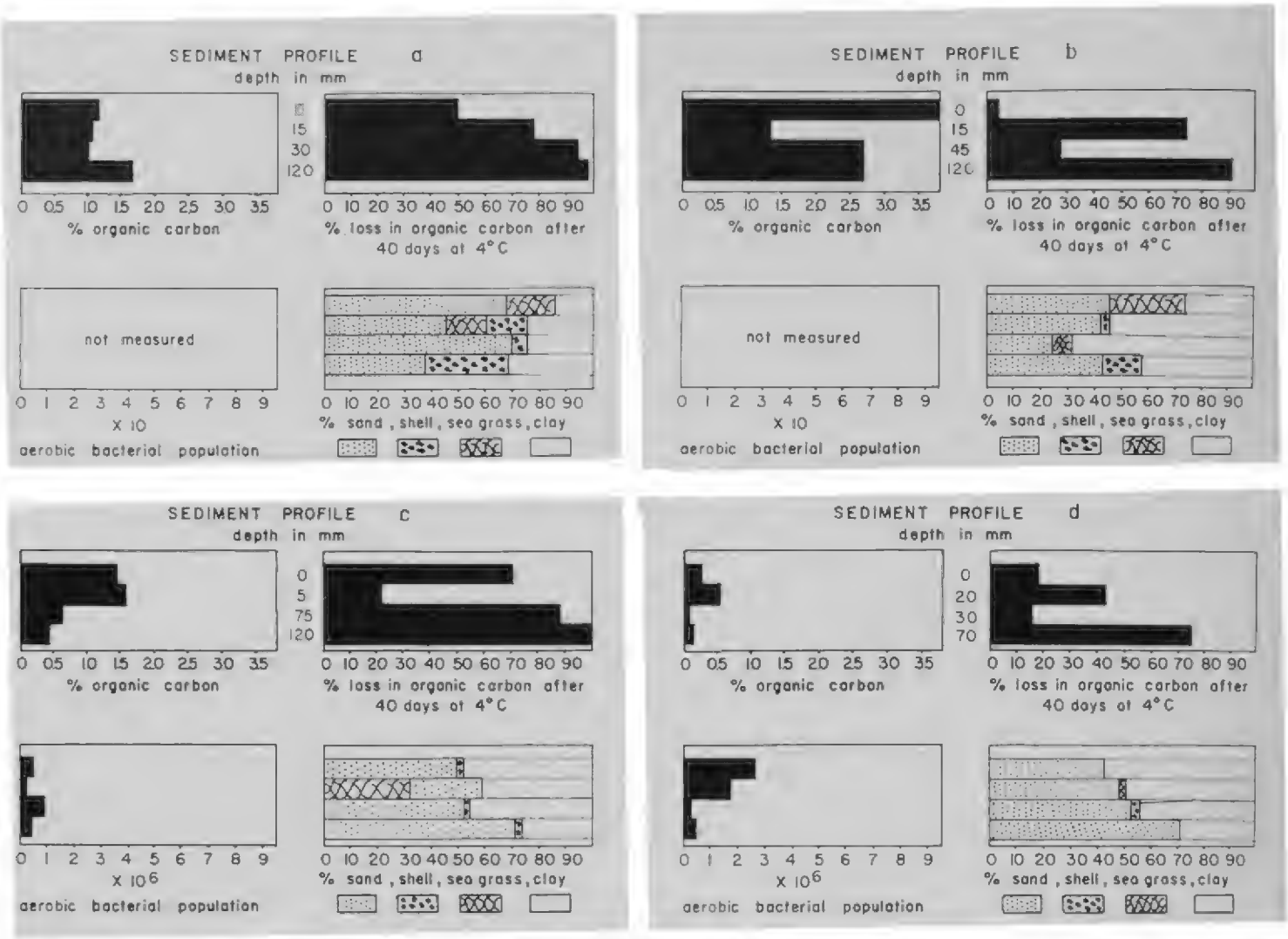
SEDIMENT PROFILE a
depth in mm
0 15 30 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
not measured
0 1 2 3 4 5 6 7 8 9
X 10
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
0 15 45 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
not measured
0 1 2 3 4 5 6 7 8 9
X 10
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0 5 75 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE d
depth in mm
0 20 30 70
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 4. Analysis of sediments from station 1 during (a) and (b) October, (c) November and (d) January, 1958.

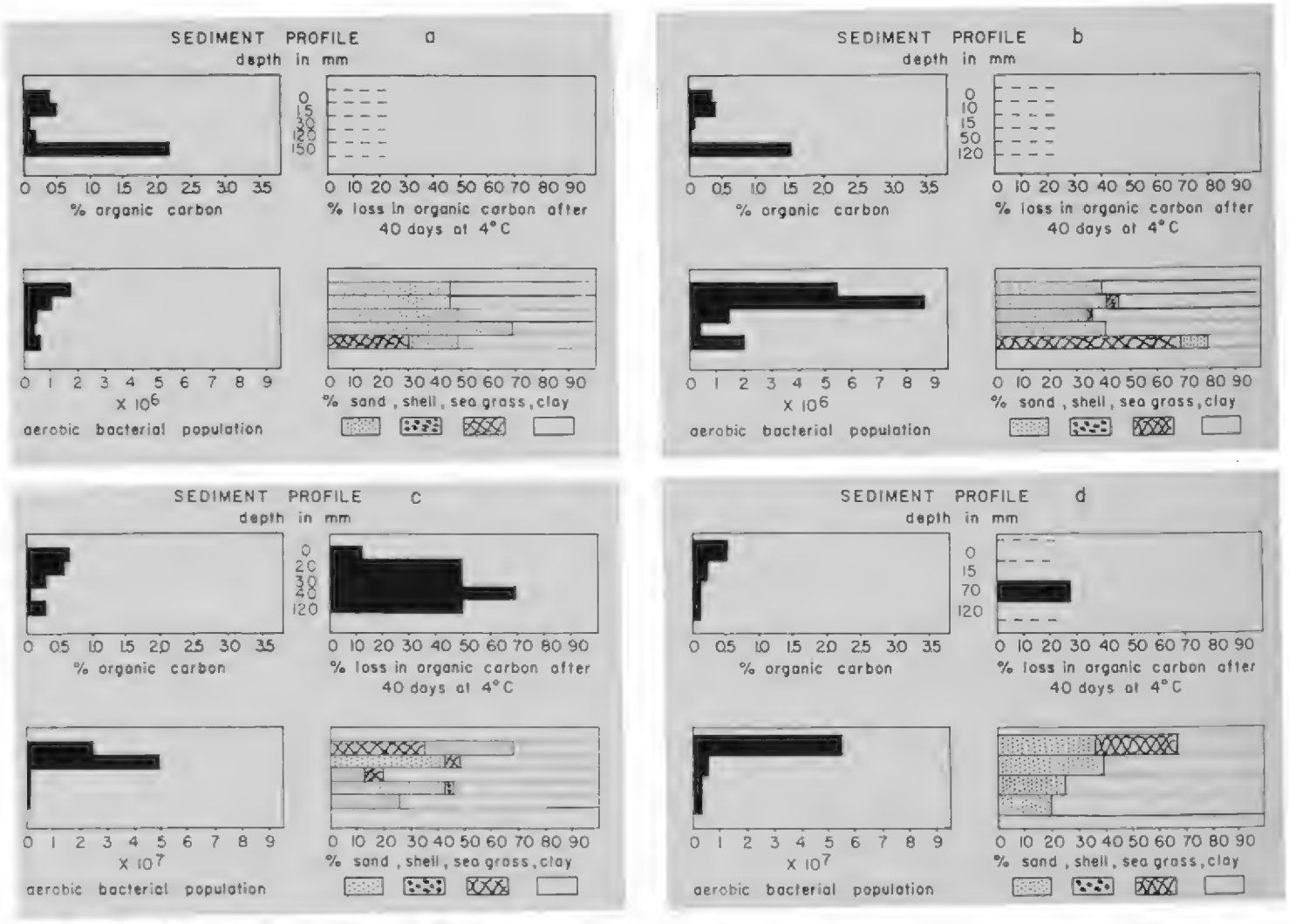
SEDIMENT PROFILE a
depth in mm
0 15 30 120 150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
0 10 15 50 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0 20 30 40 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE d
depth in mm
0 15 70 120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 5. Analysis of sediments from station 1 during (a) January, (b) February, (c) March and (d) April 1959.

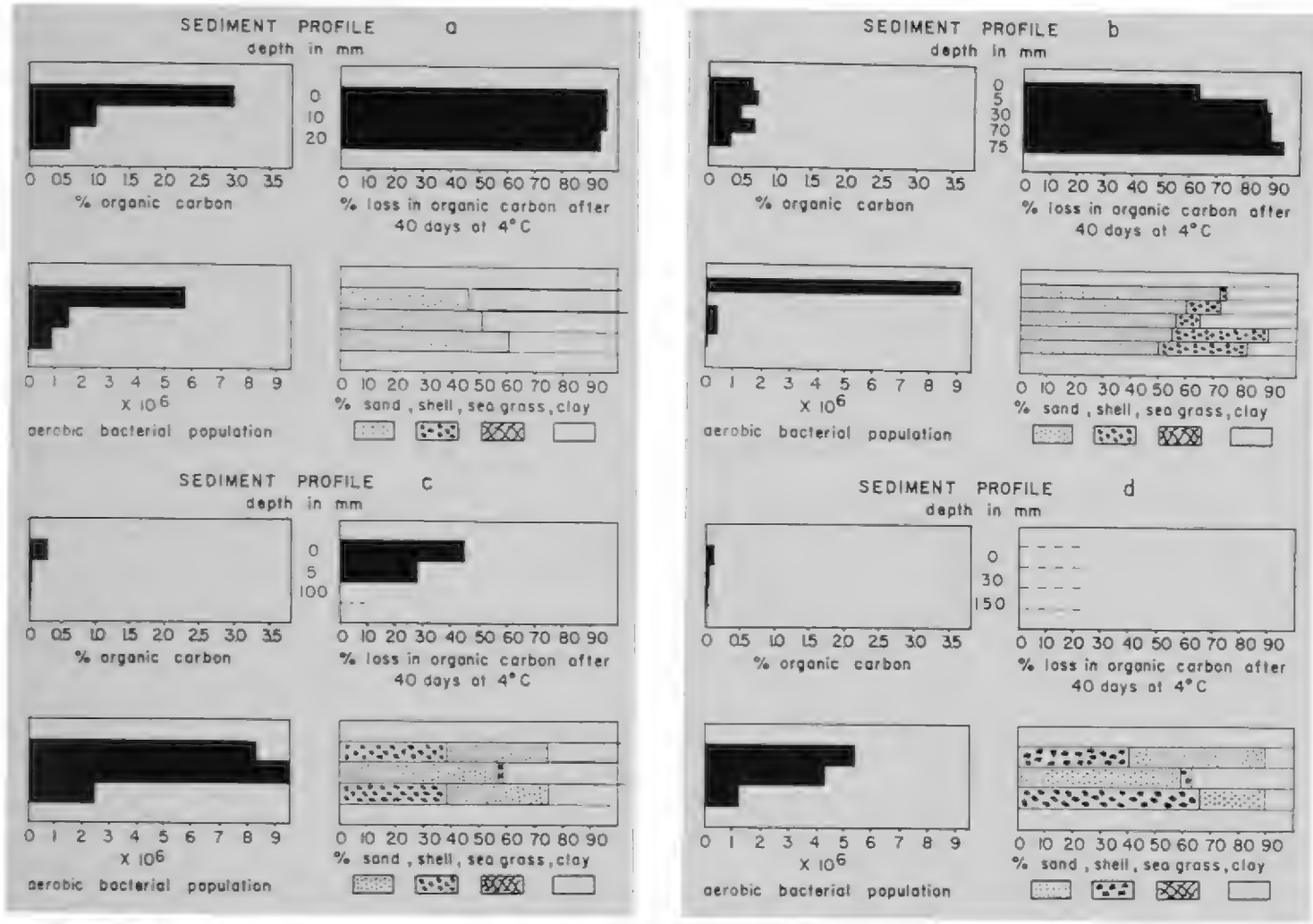

FIG. 6. Analysis of sediments from station 2 during (a) October, (b) November, (c) December and (d) January 1958–59.

DISTRIBUTION OF ORGANIC CARBON

The organic carbon content of various sedimentary types and layers is not homogenous over the limited areas studied. Sediments, separated by a few centimeters in depth or lateral area, differ appreciably in their carbon content. The type of deposited organic matter, texture of the sediments, time of year, and depth of sample are some of the factors which affect the residual concentration of organic carbon in the sediments.

The carbon content of a sediment profile does not decrease consistently with depth of sampling. In slightly more than half of the shore profiles, at least one subsurface sample contains more organic carbon than the surface layer (sediment profiles: Figs. 3b, 3c, 4a, 4d, 5a, 5b, 6b, 8a, 8b, 8c, 9c). Where an increase in carbon with depths was found, the sedimentary layer was usually associated with either a sea grass fraction or a high shell content. The station 2 area, which had the most homogeneous profile, usually showed a steady decrease in organic carbon with sample depth.

The bay samples had organic carbon contents up to 3.5%, a concentration approximately two times higher than the October surface shore samples and ten times higher than the winter values. The sea grasses in the surface bay samples account partially for the high carbon values. The subsurface layers of the bay samples appear to have large amounts of refractory material. During the winter months when carbon values below 0.1% were recorded for the shore samples, the bay sediments had subsurface carbon values of approximately 1%. The sediments there may have had a more stable environment than in the shore areas thus accounting for the large amount of organic matter.

Sea grass entrapped in the sediment accounted for an appreciable amount of the organic carbon measured, but seemed quite refractory to bacterial activity. Coarse sea

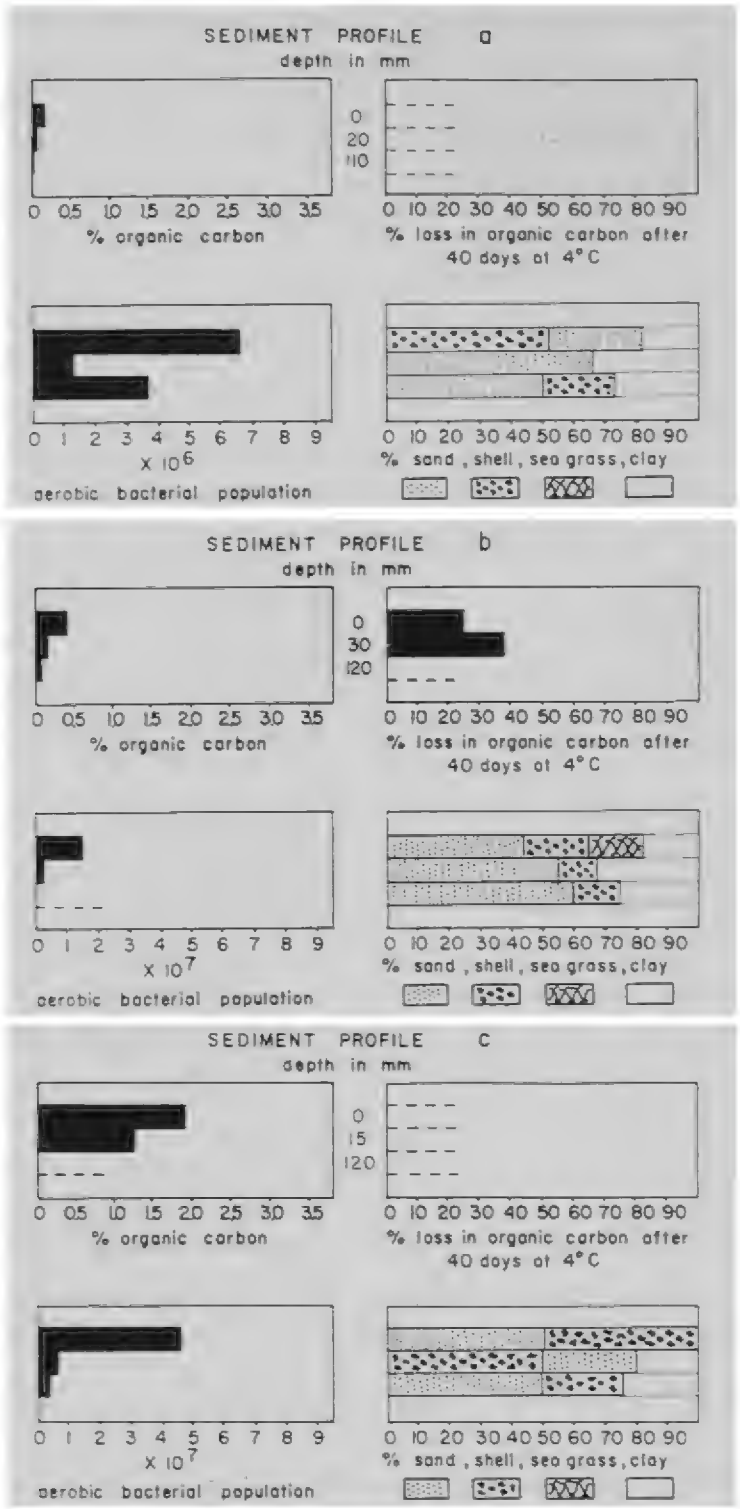
SEDIMENT PROFILE a
depth in mm
0
20
110
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
0
30
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0
15
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 7. Analysis of sediments from station 2 during (a) February, (b) March and (c) April 1959.

grass was quite common in Redfish Bay and therefore it was difficult to relate sediment size to the decomposition of the other less refractory types of organic matter. It was impossible with the procedures used to separate the sea grass from the other organic matter.

EFFECT OF SEDIMENT TYPE ON BACTERIAL DECOMPOSITION OF ORGANIC CARBON

Organic matter in the coarser sediments appeared to be more easily decomposed than organic matter in the finer sediments. Sediments with 40–50% coarse-grained material show a 58% loss in carbon after 40 days, while samples with 80–98% coarse material had an average loss of 89%.

Several factors might explain the slower rate of decomposition and loss of carbon ob-

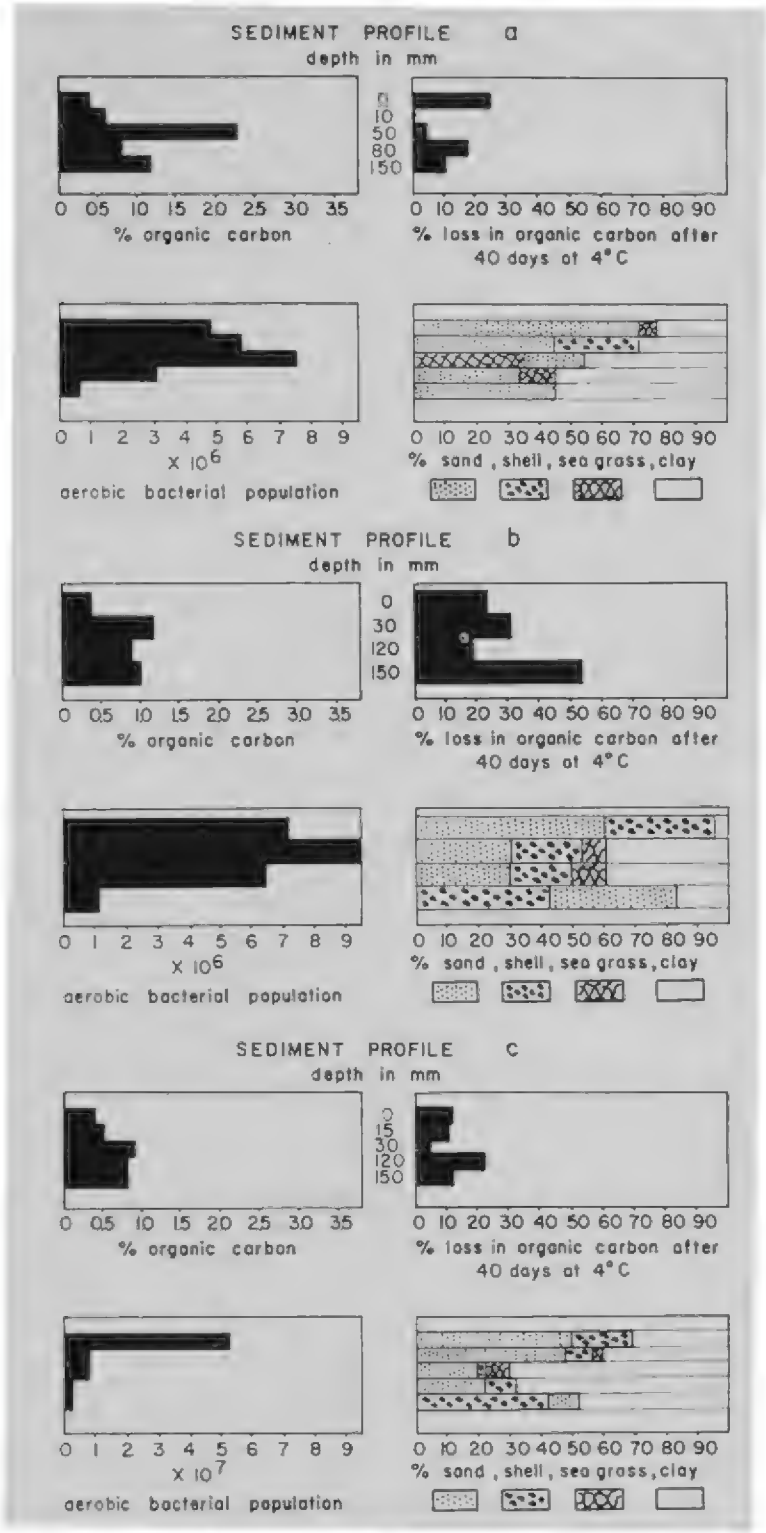
SEDIMENT PROFILE a
depth in mm
0
10
50
80
150
0 05 10 15 20 25 30 35
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
x 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand , shell , sea grass , clay
SEDIMENT PROFILE b
depth in mm
0
30
120
150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
x 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand , shell , sea grass , clay
SEDIMENT PROFILE c
depth in mm
0
15
30
120
150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
x 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand , shell , sea grass , clay

FIG. 8. Analysis of sediments from station 3 during (a) January, (b) February and (c) March 1959.

served in the clays: 1. The greater adsorptive capacity of the clay minerals affects the rate at which organic matter is decomposed (Ensminger and Gieseking, 1939). The adsorption of both organic matter and bacteria on a clay or fine particle surface might be expected to enhance decomposition, but Mortland and Gieseking (1952) found that enzymes, necessary for the decomposition process, may also be adsorbed and inactivated by association with clay minerals. 2. The complex organic matter may be broken down to smaller water-soluble organic molecules. These molecules, which can then be washed from the larger interstitial spaces of the sands by wave action, capillary action, or by compaction, may be adsorbed by the smaller clay particles. 3. The compactness of the clay minerals may present a physical barrier which limits the types and movements of bacteria. Thus, toxic by-products may accumulate, and the fewer types of bacteria may not be capable of completely mineralizing the organic matter. 4. Complex organic com-

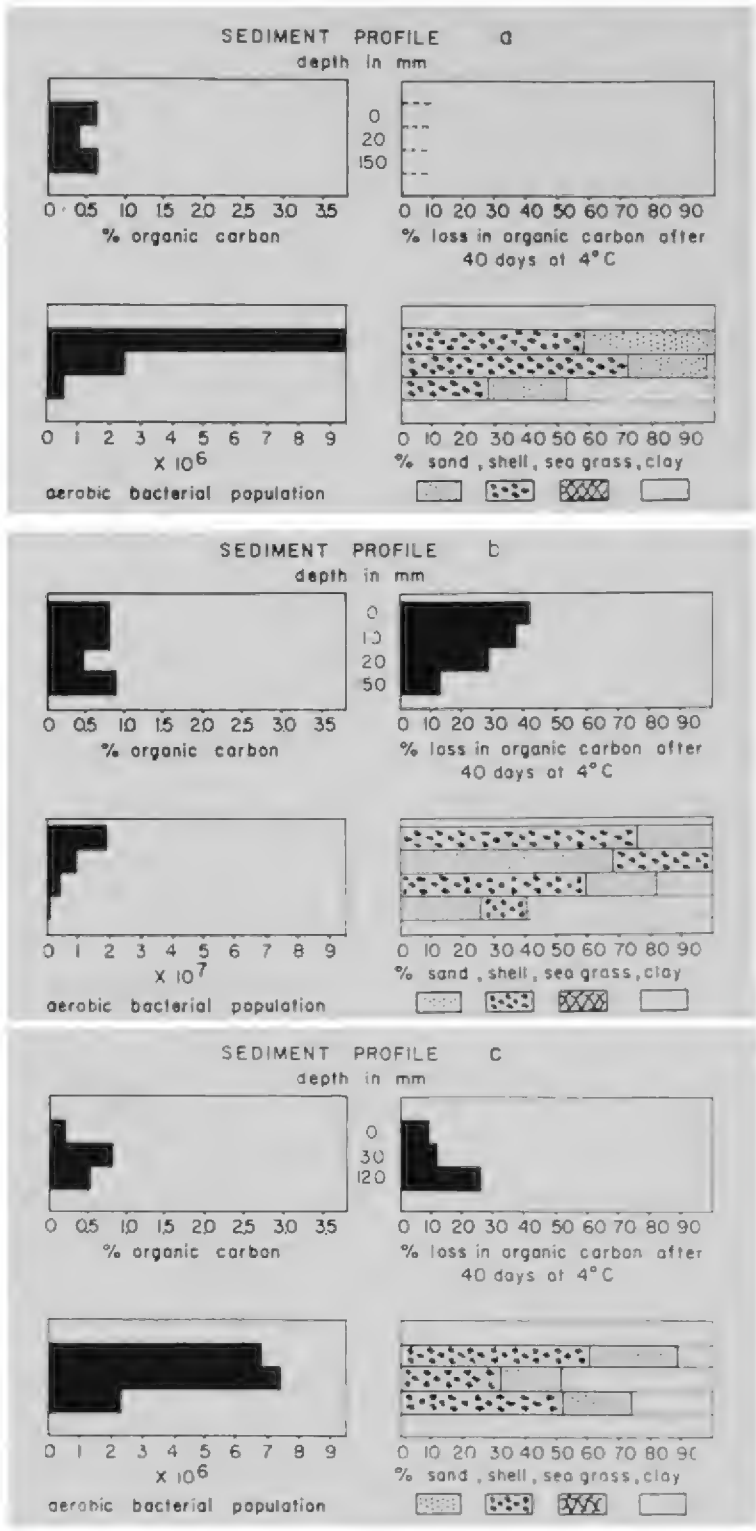
SEDIMENT PROFILE a
depth in mm
0
20
150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
0
10
20
50
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0
30
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^6
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 9. Analysis of sediments from station 4 during (a) January, (b) February and (c) March 1959.

pounds, such as the sea grasses which are associated with the clays in this study, are slowly decomposed by bacteria (Lynch and Cotnoir, 1956).

The effect of particle size on the decomposition rate may explain why sands contain less organic matter than clays as found in recent and ancient sediments (ZoBell, 1946).

DISTRIBUTION OF BACTERIA

The coarse surface sediments (sediment profiles: Fig. 6b, 6c, 6d, 7a, 8c, 9a, 9b, and 9c), when compared with the corresponding monthly bacterial counts for the clay environments, have larger bacterial populations. The inaccuracies of the plate count method could account for the larger populations recorded for the coarse shore sediments. Waksman and Vartiovaara (1938) noticed that sands, though containing a smaller bacterial population than clays, often give higher plate counts because of the separation

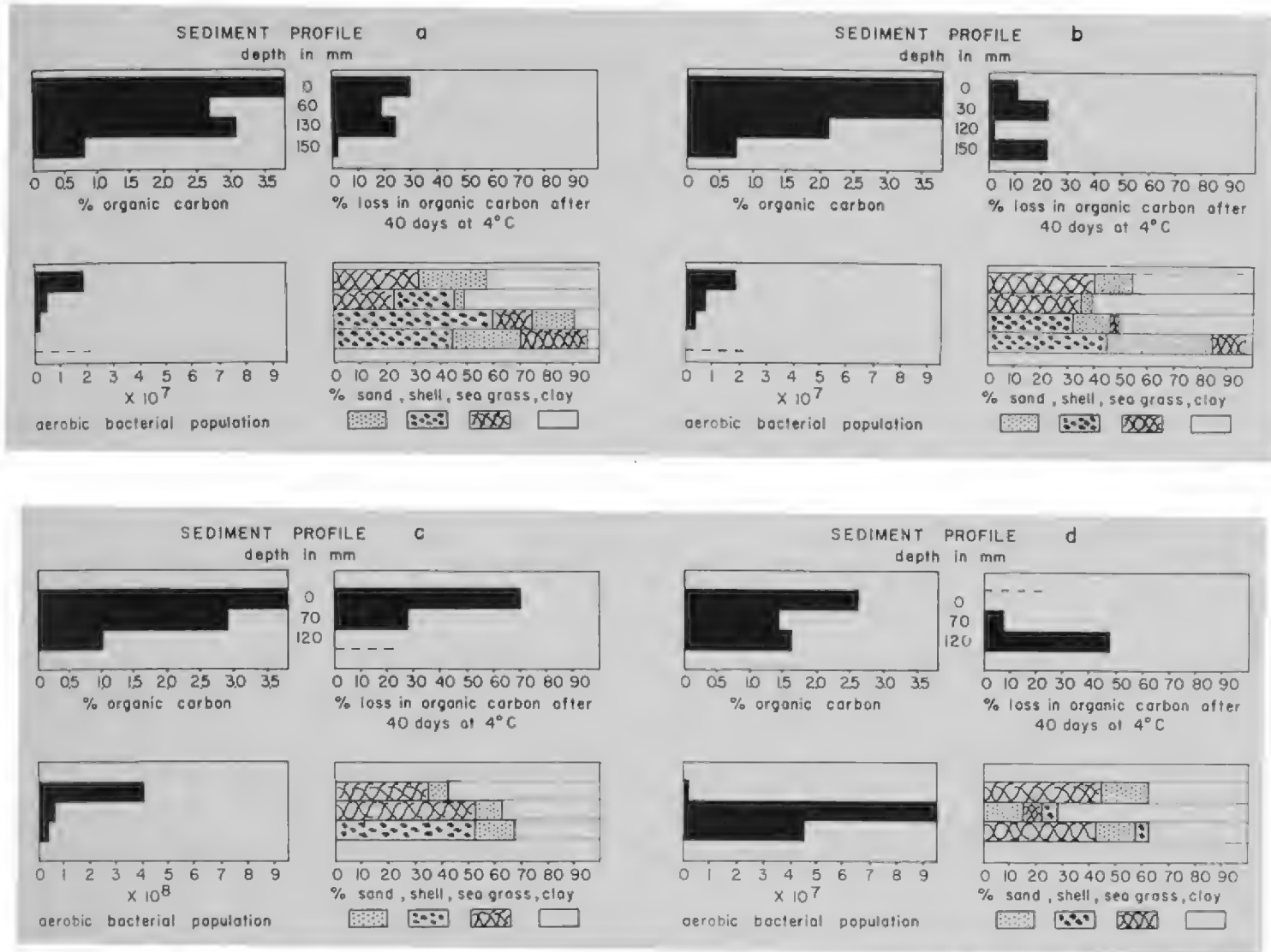
SEDIMENT PROFILE a
depth in mm
0
60
130
150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE b
depth in mm
0
30
120
150
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE c
depth in mm
0
70
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^8
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay
SEDIMENT PROFILE d
depth in mm
0
70
120
0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
% organic carbon
0 10 20 30 40 50 60 70 80 90
% loss in organic carbon after 40 days at 4°C
0 1 2 3 4 5 6 7 8 9
X 10^7
aerobic bacterial population
0 10 20 30 40 50 60 70 80 90
% sand, shell, sea grass, clay

FIG. 10. Analysis of sediments from station 5 during (a) (b) February, and (c) (d) March 1959.

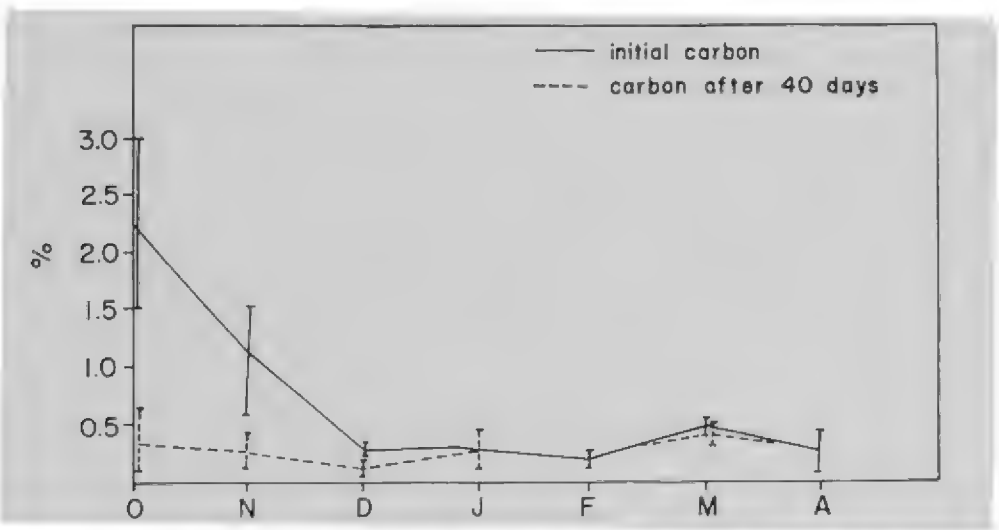

FIG. 11. Seasonal changes in organic carbon. Average of surface carbon values from stations 1 and 2.

of clumps of bacteria into individual cells by shaking with the sand grains. The adsorption of bacteria on the clays is also responsible for the lower bacterial counts of the clay environments because aggregates of bacteria on a clay particle may produce a single colony upon plating.

The bacterial numbers do not decrease consistently with sample depth. Subsurface layers of a profile often have the largest bacterial populations (sediment profiles: Fig. 4c, 5b, 5c, 6c, 8a, 8b, 9c, and 10d). An increased population is usually associated with a discontinuous sediment profile. In sediment profiles of a more homogenous texture, the bacterial numbers do decrease with sample depth.

Seasonal Variation of Bacteria and Carbon

The data indicate there is an apparent correlation between the seasonal changes and the numbers of aerobic bacteria as determined by plate counts. The higher plate counts in spring (Table 1) are reflective of the increase in decomposition. Some seasonal change in the morphological types of bacteria can be noted in the shore samples as observed by direct phase microscopic observations. There is a distinct change from predominant rod forms to several other types of microorganisms.

The organic content of the surface sediments is more subject to seasonal changes. Seasonal variations of surface organic carbon content (average of stations 1 and 2) are given in Fig. 11. Data for loss of carbon after 40 days incubation at 4°C are also given. The highest organic carbon value, 2.2%, was found in October, whereas, in February the lowest value, 0.27% (Fig. 11), was found. The organic content increased in March, but decreased again to 0.32% in April. Between the March and April sampling dates there was a seasonal wind shift to the south and with it an elevation of water level of Redfish Bay, covering the sample area with 8 cm of water. The turbulent water conditions accompanying the change of wind direction may have disrupted the developing algal communities, resulting in the lower carbon in April.

The organic carbon in the samples stored at 4°C for 40 days had carbon concentrations approximating the initial carbon in the winter samples (Fig. 11). In general, the stored samples have carbon contents of approximately 0.3% after 40 days, like the initial carbon values obtained for December, January, and February. The organic carbon in the winter samples did not decrease significantly after the 40 days storage, suggesting that only refractory organic matter remained.

A seasonal trend in organic carbon was also observed in the subsurface layers of a sediment profile. The initial organic carbon was highest in October, measuring 0.8%, declining in November to 0.5%, and then fluctuating between 0.04 and 0.07% during the winter months. In April the carbon was present in quantities too small for measurement.

The stored samples of the subsurface layers had carbon contents after 40 days which correspond to the initial organic carbon of the winter samples. It can be suggested tentatively a large amount of non-refractory organic matter may be buried during the summer months and then quickly covered with sediment. Where sedimentation occurs rapidly in the winter, when only refractory organic matter is present in the surface layers, one would expect only refractory organic matter in those representative deeper layers.

It appears that during the summer where light is available, organic matter accumulates in the surface sediments from photosynthesis of unicellular plants and during the winter it is decomposed. This implies that photosynthesis exceeds respiration during the summer, but reverses during winter when respiration predominates over photosynthesis and causes the organic matter to decrease. The data from plate counts (Table 1) indicate that the bacterial populations remain at a somewhat constant level during the fall and winter months and increase during spring.

Microbial Activities

It is impossible to predict the amount of microbial activity possible in a sedimentary environment without knowing how accessible the organic carbon is to the bacterial

population. An indication of bacterial activity in sediments may be obtained by observing a loss in organic carbon during storage, assuming that loss in organic matter is due largely to bacterial action.

If loss in organic carbon is a result of bacterial activities, plate counts are not reliable as indicators of microbial activity because no correlation was observed between loss in organic carbon after 40 days and the bacterial plate counts.

The decrease in the amount of organic carbon during storage at 4°C indicates bacteria are active during the winter months. In January and February, much of the organic matter must be decomposed or refractory as the decrease in carbon loss indicates a decrease in bacterial activity.

One of the most interesting results is the large amount of apparent microbial activity during storage of samples at 4°C. Our results indicate that appreciable alteration of sediment will occur following such refrigeration.

Conclusions

1. The shoreline sediments in Redfish Bay are not uniform either horizontally for distances greater than 1 meter or vertically to a depth of approximately 20 cm. Monthly profile samples collected from single stations show differences in texture, bacterial counts and organic carbon.

2. The organic carbon does not decrease or increase consistently with depth. Where an increase in carbon with depth is measured, the sedimentary layer is usually associated with either a sea grass fraction or a high shell content. Organic carbon varied from 3.7 to 0.1 per cent dry weight.

3. The bay sediments contain large amounts of refractory organic material which are decomposed rather slowly.

4. The organic matter in the coarser sediments appears to be more easily decomposed. The complex organic matter usually associated with the clay minerals, the high degree of compaction, and the greater adsorptive capacity of clay sediments may explain the slower rate of decomposition observed.

5. The coarse surface sediments usually have larger bacterial populations than the clays as measured by the plate count method. The bacterial numbers do not decrease consistenly with depth. An increased population in a subsurface layer is usually associated with a discontinuous sediment profile.

6. The data indicate that bacterial numbers increase in the spring when the temperature rises.

7. Seasonal changes in the initial organic carbon are observed in surface and subsurface sediments, with the highest organic carbon measured in October and the lowest in February. In general, the samples stored at 4°C for 40 days have carbon contents which correspond to the initial carbon values obtained for December, January, and February. Loss of carbon during incubation at 4°C varied from 0 to 95 per cent.

8. Refrigeration is not a satisfactory method by which sediments may be stored and transported in their original state. Samples stored at 4°C continue to be altered appreciably by bacterial activity.

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Some Aspects of Osmotic and Ionic Regulation in the Blue Crab, *Callinectes sapidus*, and the Ghost Crab, *Ocypode albicans*[1]

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Abstract

Analyses were made of constituents of body fluids in the ghost crab, *Ocypode albicans*, and the blue crab, *Callinectes sapidus*, relative to hypo and hypersaline environments in the bays of south Texas. Blood and urine concentrations of Na, K, Ca, Mg, Cl, and SO_4 are given for *Ocypode albicans* in concentrations from 14 to 197 percent sea water (% S.W.). All ions are regulated to some extent at all salinities. At temperatures above 29° C the ability of *Ocypode* to regulate blood Na and total molar concentration is reduced. In *Uca* (from Massachusetts), blood osmotic concentration is lower (in 190% S.W.) at 21° than at 10 or 30° C. Neither *Ocypode* nor *Uca* can survive in 190% S.W. at 30° C for more than a few days, but both species can withstand this salinity for at least two weeks at 20–25° C. Decreased urine Na concentrations occur in *Uca pugnax*, *Ocypode albicans*, and *Cardisoma guanhumi* when subjected to hypersaline stress. In *Ocypode* the effect is most pronounced at high temperatures. In both *Ocypode* and *Uca*, injection of $MgCl_2$ lowers urine Na if it is initially high, raises it if it is initially low.

Callinectes sapidus has limited hypo-regulatory ability for total blood concentration, and marked ability to regulate blood magnesium and sulphate in high salinity, both in the Laguna Madre and in the laboratory. *C. sapidus* from the Laguna Madre seem to withstand combined high temperature and high salinity better than do other crabs investigated. *C. sapidus* from the high salinity lagoon are more tolerant of high salinity, and less tolerant of low salinity, than are crabs from a brackish river, at least in summer; evidence for a genotypic difference is not conclusive.

Ratios of stomach fluid to blood for magnesium, sulphate, and osmotic concentration are much higher than the same ratios for other ions in both *Callinectes* and *Ocypode* and indicate that the digestive tract may take part in regulation of Mg and SO_4 in the blood.

Introduction

Studies of regulation of osmotic and ionic concentrations of the blood of marine crustacea have been concerned mainly with hyper-regulation, *i.e.*, regulation in dilute sea water, where internal concentrations are maintained higher than in the external environment. Observations of hypo-regulation, where internal concentration is maintained lower than the external environment, are less frequent. Several works are available on ionic and osmoregulation in crustacea (Prosser, Green, and Chow, 1955; Beadle, 1957; Robertson, 1957, 1960; Schlieper, 1958; and Nicol, 1960).

Many Crustacea common to brackish water have been found to hyporegulate when exposed to full strength or slightly concentrated sea water. Among these are the shrimp, *Crangon crangon* (Broekema, 1941); several species of the prawn, *Palaemonetes*, (Panikkar, 1941; Parry, 1954); and the estuarine crabs, *Holoecius cordiformis* (Ed-

[1] From a dissertation submitted to the Graduate College of the University of Illinois in 1958 in partial fulfillment of the degree of Doctor of Philosophy under the supervision of Dr. C. Ladd Prosser. The study was conducted during 1956 at the Institute of Marine Science, Port Aransas, Texas with a stipend from The University of Texas.

monds, 1935), *Eriocheir sinensis* (Conklin and Krogh, 1938, and *Callinectes sapidus* (Odum, 1953); although in the last species blood osmotic concentrations were measured after only one day's exposure to concentrated sea water.

Hypo-regulation has also been reported for crabs occupying a terrestrial or semi-terrestrial habitat. Several species of land crabs were reported by Pearse (1932) to show hypo-regulation of blood osmotic concentration. Other studies, some of them including evidence of hypo-regulation of individual ions, have been made for *Pachygrapsus crassipes* (Baumberger and Olmstead, 1928; Gross, 1955, 1957; Prosser *et al.*, 1955); *Uca crenulata,* (Jones, 1941); *Uca pugnax and U. pugilator* (Green *et. al.*, 1956, 1959); and *Ocypode albicans* (Flemister and Flemister, 1951; Flemister, L., 1958; Flemister, S., 1959). All of these animals can also hyper-regulate and can live in dilute sea water.

Hypo-regulation in *Palaemonetes* (Parry, 1954), *Pachygrapsus* (Prosser *et al.*, 1955), and *Uca* (Green *et al.*, 1946) appears similar in that the antennary gland does not function in osmotic hypo-regulation, but assists in regulation of magnesium and sulphate. Both of these ions are well regulated in the bloods of all three animals under hyper-saline stress. In *Pachygrapsus* and *Pachygrapsus* and *Uca* exposure to high external salinities is associated with a decrease in urine sodium; this does not occur in *Palaemonetes.* In *Pachygrapsus* the decrease in urine sodium was abolished by placing crabs in artificial concentrated sea water in which the magnesium was replaced by sodium; magnesium excretion was thought to interfere in some way with sodium excretion.

An unusual opportunity to study the natural occurrence of hypo-regulation in Crustacea is presented by the Laguna Madre, a landlocked bay on the Gulf coast of Texas, in which a marine-estuarine fauna is regularly subjected to hyper-saline stress. The Laguna Madre has been described from several viewpoints by a number of investigators; among these are: Hedgpeth (1947, 1953), Collier and Hedgpeth (1950), Ladd (1951), and Simmons (1957). The features of large surface area, shallow depth, high temperature and rate of evaporation, limited fresh water drainage, and limited exchange with open bays or the Gulf of Mexico combine to produce commonly salinities of 60 ‰ and temperatures of 35°C. The most important crustacean in the Laguna is the copepod, *Acartia tonsa,* but several species of prawns and shrimp, and the crabs *Callinectes sapidus* and *C. danae* are encountered under moderate salinity and temperature stress. *Uca pugilator* lives on mud flats adjacent to the Laguna. All of the invertebrates found in the Laguna are also found in brackish water, i.e., they can all withstand low salinity, as pointed out by Hedgpeth (1953).

In this paper possible differences in specific ion regulatory mechanisms in land and aquatic Crustacea under hyper-saline stress were investigated using *Ocypode albicans, Callinectes sapidus,* and *Uca pugnax.* The degree of hypo-regulatory ability of *Callinectes sapidus,* a cosmopolitan species found in the Laguna Madre, was compared with other members of the species found outside of the Laguna.

Materials and Methods

Fiddler crabs, *Uca pugnax,* were obtained from mud flats surrounding a land-locked lagoon near Rockport, Texas, and kept in dishes filled to a depth of about a centimeter

with sea water. Experimental animals were fed fish once a week and their water was changed about every 3 days.

Ghost crabs, *Ocypode albicans*, were trapped on the Gulf Beach of Mustang Island. Crabs were kept in plywood boxes containing six inches of clean dry sand with about one crab per square foot. Pans of sea water were buried flush with the sand surface.

A few land crabs, *Cardisoma guanhumi*, were obtained from Rockport and maintained in a similar manner.

Blue crabs, *Callinectes sapidus*, were collected from high salinity stations in the Laguna Madre, from intermediate salinity stations at Port Aransas, and from low salinity waters at the mouth of the Guadalupe River in San Antonio Bay and kept in tanks containing sea water.

All crabs were immobilized, for sampling of body fluids, by fastening them to mounting frames. Crabs suffered no apparent injury even when tied to these frames for several hours.

High salinity water was obtained from the Laguna Madre or concentrated by evaporation.

Blood was sampled by syringe (without anti-coagulant), or by puncture with melting point capillaries. Urine was sampled by suction through a fine glass tip into a collecting trap, with the operculum retracted with a fine glass hook. Stomach fluid was collected with a syringe fitted with the heaviest practical polyethylene tubing.

Analytical Methods

Osmotic pressure was measured by comparing melting point depression of unknown solutions with NaCl standards in capillary tubes (Gross, 1954).

Chloride was determined by the modification of the mercurimetric method of Scribner (1954) involving titration with $Hg(NO_3)_2$ using diphenylcarbazone as an indicator. When the acidified sample is titrated with $Hg(NO_3)_2$, the mercury joins with the chloride to form soluble but non-ionized $HgCl_2$. The first excess of mercury reacts with diphenylcarbazone to form a deep purple complex at the endpoint. Reagents used were: (a) 1.000 N NaCl solution used for standardization. (b) 0.1 N. $Hg(NO_3)_2$, (34.264 gm $Hg(NO_3)_2$ H_2O was dissolved in 100 ml water and 2 ml HNO_3 and diluted to 1 liter). (c) Diphenylcarbazone indicator, (400 mg was dissolved in 100 ml of 95% ethyl alcohol and kept in a lightproof bottle under refrigeration). (d) 0.1 N HNO_3, (7.0 ml fresh concentrated nitric acid diluted to 1 liter).

When larger volumes were present, 0.1 ml samples were titrated in test tubes with a syringe burette fashioned from a tuberculin syringe (Scholander, 1947). The sample was added to 4–5 ml water and made acid with 5 ml of N/10 nitric acid to a pH below 2. Three or four drops of indicator were added and titration conducted. For small amounts precision micropipettes were used. A one lambda sample, 5 lambda of indicator, and about 25 lambda of N/10 nitric acid were added to a 50 lambda drop of water on the paraffin block (Fig. 1) and titrated with the microburette shown in Fig. 1. Determinations of 0.5 milliequivalents of chloride were made with an accuracy of 1% or of 0.5 microequivalents within 5%. For field salinity determinations, the method compares favorably with hydrometers in speed, convenience, and accuracy. It agrees quite well with the Mohr method and in blood samples it avoids the necessity of deproteinization (Table 1a).

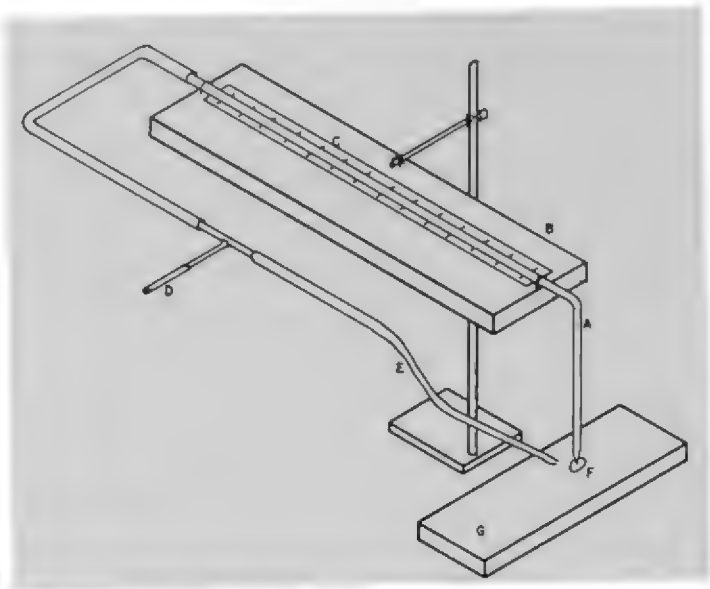

FIG. 1. Microburette used in chloride determinations. A, burette; B, board; C, metric ruler; D, mouthpiece; E, pressure control tube and air for stirring; F, titration drop; G, paraffin block.

TABLE 1a

Comparison of Cl titration using $Hg(NO_3)_2$ with titration using $AgNO_3$. All values are mM/l

Sample	$AgNO_3$ 10 ml sample	$Hg(NO_3)_2$ 0.1 ml sample	$Hg(NO_3)_2$ 0.001 ml sample
1	531.11	532.7	536
	531.59	532.7	530
	531.40	532.3	529
	532.08	.....	.....
2	544.05	545.1	538
	544.01	544.8	542
	544.16	545.3	549
3	875.22	876.1	878
	875.08	873.3	878
	875.13	874.9	872

TABLE 1b

Comparison of Cl titration of *Callinectes** blood with and without deproteinization

Deproteinized Schnor method† 0.1 ml sample	Deproteinized 0.1 ml	Not deproteinized 0.1 ml	Not deproteinized 0.001 ml
548	549	551	545
548	549	552	554
550	546	554	555

* Crab was living in a medium containing 544 mM Cl/l.
† Schnor, 1934.

Sulfate was determined by a modification of the turbidometric method of Nalefski and Takano (1950). Sulfate was precipitated as $BaSO_4$, and turbidity was measured in a spectrophotometer. Particle size and stability were controlled by precipitating in a concentrated salt-acid solution. Proteins were removed by previous precipitation with uranium acetate.

Reagents used were: (a) Standard SO_4, 0.3 mg SO_4/ml, (0.5347 gms dry K_2SO_4/liter). (b) Salt-acid, (240 gm NaCl, 20 ml concentrated HCl/liter). (c) Uranium acetate, (0.5% aqueous solution). (d) $BaCL_2$ fine mesh crystals.

Three ml of salt-acid solution and from zero to 2.0 ml SO_4 standard (0 to 0.6 mg SO_4) were placed in each of a series of 11 standard tubes and diluted with H_2O to a total volume of 5 ml. A graded standard series was used, at 0.2 ml intervals. Three ml of salt-acid solution were placed in each unknown tube. A sample (2 ml), containing from zero to 0.6 mg SO_4 was added, and contents were diluted to 5.0 ml with water.

Protein was removed before samples were added to the salt-acid solution to avoid forming a precipitate other than $BaSO_4$. Tenth ml samples of blood were deproteinized by adding them to 0.3 ml of 0.5% uranium acetate and 0.6 ml H_2O in a 15 ml centrifuge tube and centrifuging. The precipitate was washed twice with 0.5 ml portions of H_2O. Supernatant and washings were then handled as above. The precipitate was dried and weighed to give a rough estimate of protein concentration of the blood.

All tubes were shaken until contents were thoroughly mixed. Contents of all tubes which were not perfectly clear were discarded. Enough $BaCl_2$ was added to each tube so that after thorough shaking a few crystals remained in the bottom of the tube.

Samples were read in the spectrophotometer at 400 millimicrons within 1 hour. The $BaSO_4$ suspension was stable for this period. After several hours the precipitate settled to the bottom, but corked tubes shaken up and reread at 1 and 2 days after precipitate formation showed no change. Calibration curves were prepared by plotting Mg SO_4 (in standard tubes) against optical density.

Standard curves prepared using the Coleman Jr. Spectrophotometer were not smooth, but since duplicate standards prepared simultaneously usually agreed within 1% T, and the greatest deviation of any standard over a period of 9 months was 5% T, the method was considered reproducible.

The accuracy of the method was checked in the following way. Chloride concentration of seven sea water samples was determined by titration with $AgNO_3$. Sulphate concentration was determined from tables of the ionic concentration of sea water (Barnes, 1954) and compared with those obtained by the turbidometric method (Table 2).

TABLE 2

Comparison of SO_4 determinations by turbidometric and precipitation methods. All values are mEq/l

Cl	SO_4 turbidometric	SO_4 Barnes method*	Deviation percent
569	59.6	58.62	+1.67
659	67.5	67.92	—0.62
574	59.6	59.14	+0.78
671	66.8	69.10	—3.33
1041	108	107.3†	+0.65
792	83.6	81.68	+2.35
925	93.1	95.32	—2.33

* 1954.
† By extrapolation.

The method was designed for 0.1 ml samples of sea water and biological fluids of marine animals. It is rapid and simple, and requires only readily available reagents and laboratory apparatus.

Sodium and potassium were determined by flame photometer. Two instruments were used, a Coleman and a Beckman DU Spectrophotometer with flame attachment. For analysis in the Coleman, samples were diluted 1,000 times for Na and 500 times for K, and compared to suitable standards.

Calcium and magnesium were determined by the micro method of Shaw (1955) and by flame photometry using the Beckman DU with photomultiplier and hydrogen-oxygen flame.

In flame analyses, because of the small size of individual samples, and the large number of determinations to be made, all cations were determined in one sample. A single composite standard was prepared containing the various ions in the same relative concentrations in sea water, but at twice the absolute concentration. The exact concentrations in the standard solution are as follows:

	gms/l	mEq./l	ppm	Source
Na	20.4596	889.6	20460	52.0071 gms NaCl
K	.7364	18.838	736	1.4045 gms KCl
Ca	.7772	19.392	777	193.91 ml . 1N $CaCO_3$
Mg	2.4654	101.38	2465.4	Mg ribbon dissolved in 101 ml 1N HCl

The composite was more concentrated than any unknown to be analyzed. For cation analysis, the following dilutions of this standard were made: 25, 20, 15, 10, 5, and 0 lambda/10 ml H_2O. Light emission was measured for each dilution at the following wave lengths: Na, 588 mμ; K, 763 mμ; Ca, 442.7 mμ; and Mg, 383 mμ; and standard curves were prepared. Linear relationships were found for emission versus concentrations for all ions except Na, which curved downward slightly at its upper limit. Unknown solutions were diluted by adding 10 or 25 lambda of sample to 10 ml H_2O.

Validity of methods. Analysis of 11 sea water samples by these methods yielded anion to cation ratios of from 0.973 to 1.078. The average was 1.017. The methods (except sulphate) were checked for protein interference by analyzing aliquots of one blood sample before and after removal of protein by precipitation with uranium acetate. No serious interference was found.

Experiments and Results

Relationship of Internal Medium to External Medium in *Ocypode albicans*

In Figures 2–11 and Tables 3, 4, and 5 are the results of experiments in which the fluids of the ghost crab *Ocypode* were analyzed relative to various concentrations of sea water through the hypo and hypersaline ranges. Data include results of measurements of osmotic concentration, sodium, potassium, magnesium, calcium, chloride, sulphate, and protein in blood (B), in stomach fluids (S.F.), and in urine (U) from the antennary gland.

Osmotic concentrations of the blood, urine, and medium (M) in media from 25 to 180% S.W. are presented in Fig. 2. Total molar concentrations of the ions analyzed, including some cases in which osmotic concentration was not measured, are presented in Fig. 3.

Total blood concentration, as indicated by osmotic concentration and summation of ions, is well-regulated over the whole salinity range, from 14 to 197% S.W., although there is a tendency for it to decrease in low salinities and increase in very high salinities. A fourteen-fold increase in external salinity is accompanied by only a 50% increase in blood concentration. High temperature did not abolish the ability to regulate total blood

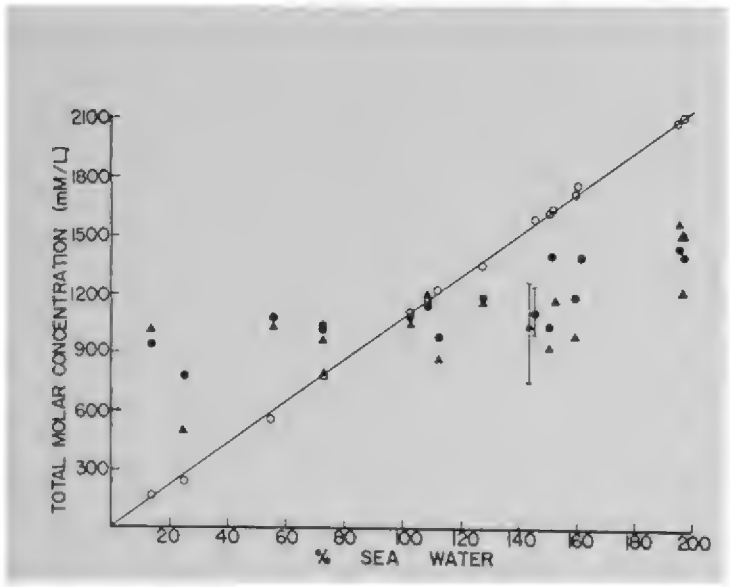

FIG. 2. Osmotic concentrations of blood (dots), urine (triangles), and medium (circles) of *Ocypode* in various sea water concentrations.

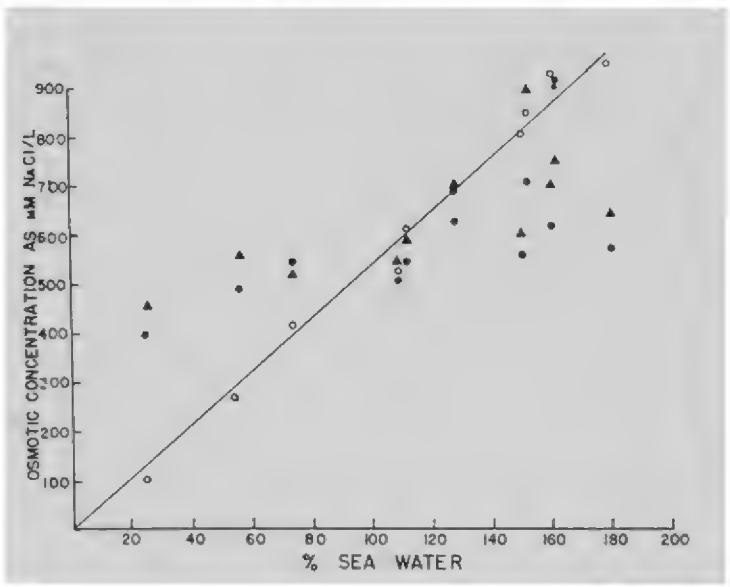

FIG. 3. Total molar concentration of blood (dots), urine (triangles), and medium (circles) for *Ocypode* in various sea water concentrations.

concentration, but B/M ratios were closest to unity at high temperatures. Blood is hypotonic to normal sea water.

The antennary gland does not seem to function in osmotic regulation. Urine osmotic concentrations are close to blood concentrations. Of 11 animals, 8 had osmotic U/B ratios greater than 1, while 3 were less than 1. The slight urine hypertonicity occurs throughout the entire range of the medium.

Sodium concentrations are graphed in Figures 4–6. Both blood Na regulation and

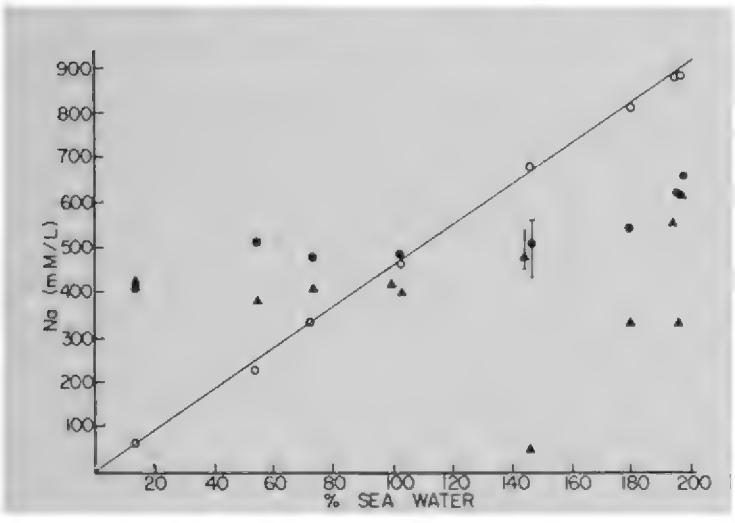

FIG. 4. Urine Na/blood Na ratios for *Ocypode* in various salinities at 12–25° C. (circles), and at 29–35° C. (dots).

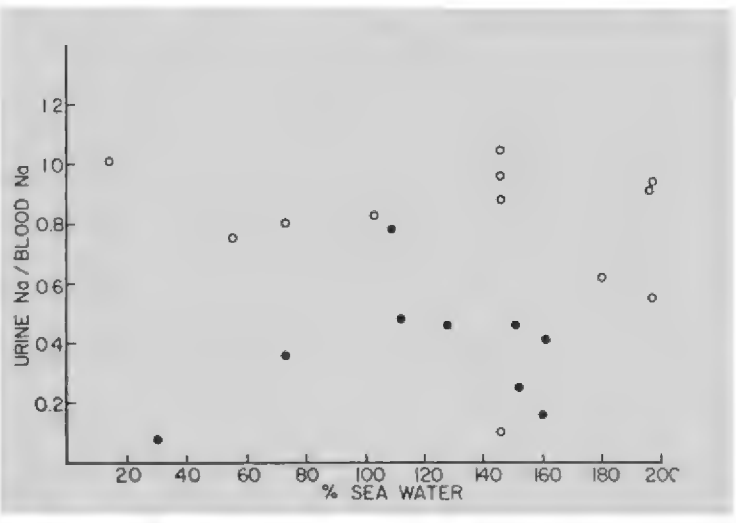

FIG. 5. Sodium concentrations in blood (dots), urine (triangles) and medium (circles) for *Ocypode* in various sea water concentrations at 12–25° C.

urinary excretion are affected by temperature. At low temperatures, blood Na is well-regulated at all salinities. At high temperatures it is less well-regulated, especially at high salinities. The points showing least regulation were all based on animals sampled between 29–35°C. At high temperatures (with one exception), urine Na is low at all salinities (Fig. 6). At low temperatures (also with one exception), urine Na is much higher (Fig. 5), although it never is as high as blood Na. This is apparent both from the graphs of the Na concentrations for the two temperature ranges and from the graph of U/B vs. salinity (Fig. 4). The two groups (with the exceptions mentioned) are completely separate. The reduction in urine Na concentration below that in blood or medium occurs in *Ocypode* at all salinities at high temperature.

Blood K concentration is held constant at about 5 mM/L in media ranging from 14 to 160% S.W. (Fig. 7). Above this, it increases but never exceeds 11 mM-L. The ability to regulate blood K is not seriously affected by temperature, although one high value (at 73% S.W.) was measured at 30°C.

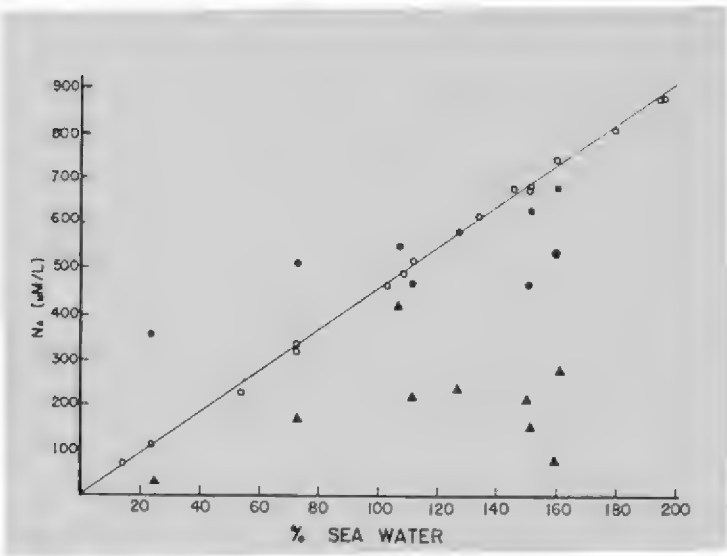

FIG. 6. Sodium concentrations in blood, urine, and medium for *Ocypode* in various sea water concentrations at 29–35° C.

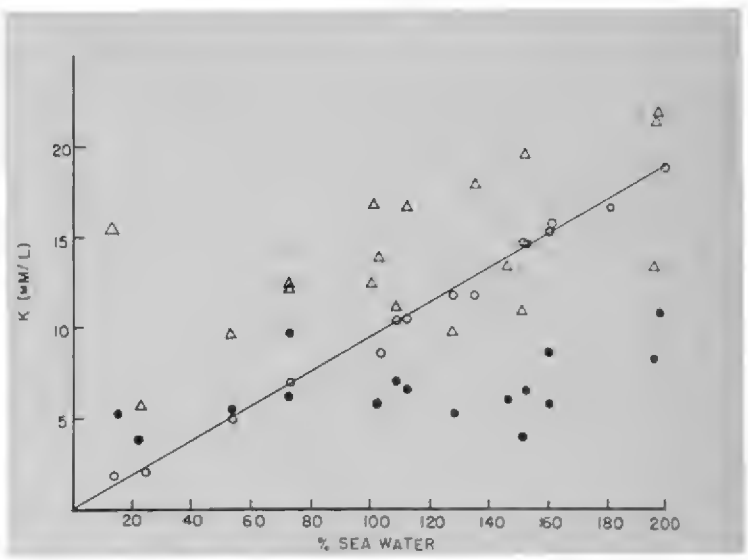

FIG. 7. Potassium concentrations from Table 7 plotted against sea water concentration. Circles represent medium, dots represent blood, triangles represent urine.

Potassium is more concentrated in urine than in blood at all salinities. Generally, it is also more concentrated in urine than in medium. The ability to excrete K in the urine is also independent of temperature. It seems likely that K excretion is an important function of the antennary gland.

In contrast to K, Ca concentration is higher in blood than in urine over the range of salinities from 14 to 161% S.W.; at 196% S.W., however, urine Ca exceeded blood Ca in two animals, and stayed low in one (Fig. 8). At low salinities B/M is greater than

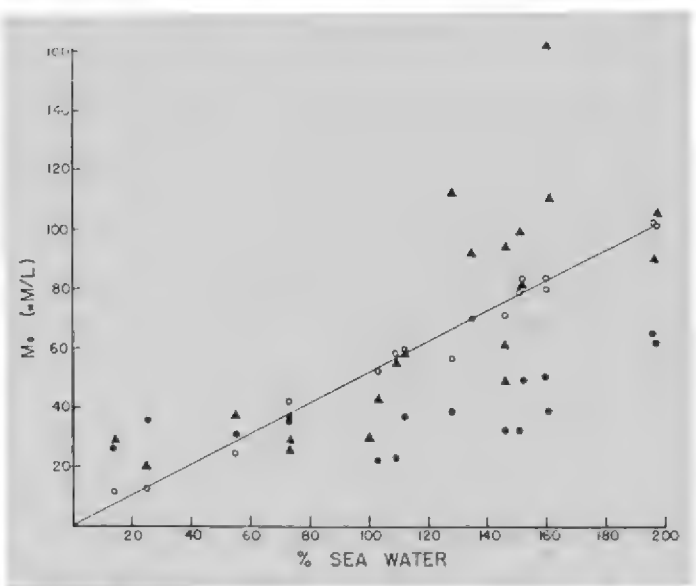

FIG. 8. Calcium concentrations for *Ocypode* blood (dots), urine (triangles), and medium (circles) plotted against sea water concentrations.

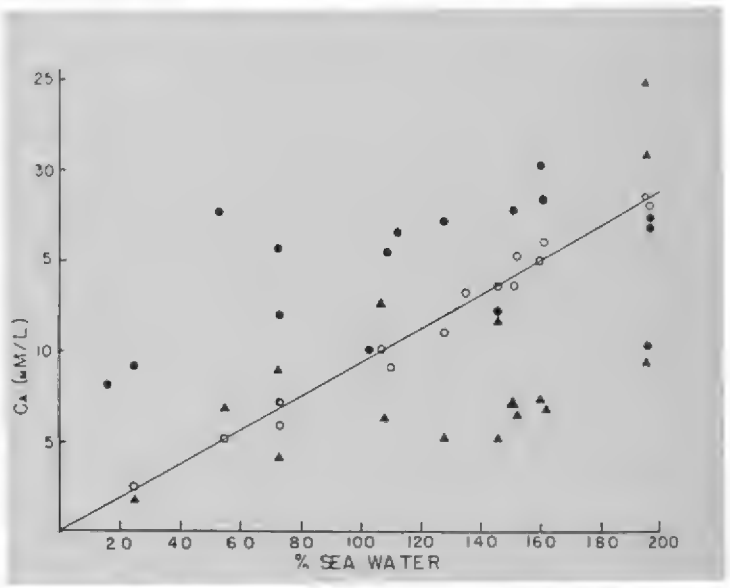

FIG. 9. Magnesium concentrations in blood (dots), urine (triangles), and medium (circles) of *Ocypode* plotted against sea water concentrations.

one at all temperatures. Blood Ca is higher than medium Ca at high temperatures and in high salinities; lower than medium Ca at low temperatures and high salinities. At high salinities, B/M is always less than unity at low temperatures, greater than one at high temperatures.

Magnesium is well-regulated in the blood (Fig. 9), although there is a noticeable upward trend in salinities above 150% S.W., and absolute values are higher than those reported (Robertson, 1953; Parry, 1954) for other active Crustacea. Blood to medium ratios are about the same at similar salinities for the two temperature ranges, indicating that regulation of blood Mg is not greatly affected by temperature.

Urine Mg is about equal to blood Mg in low salinities. In salinities above about 100% S.W., urine Mg increases. This increase is much more pronounced at higher temperatures, and seems to be associated with the simultaneous decrease in urine Na. At low salinities and high temperatures, low urine Na values were found concurrently with low magnesium concentrations; hence, both temperature and magnesium stress may affect urine Na concentration.

Blood Cl is well-regulated at all except the highest salinities (196–197% S.W.) (Fig. 10). The B/M ratios are similar for both temperature groups over the whole temperature range.

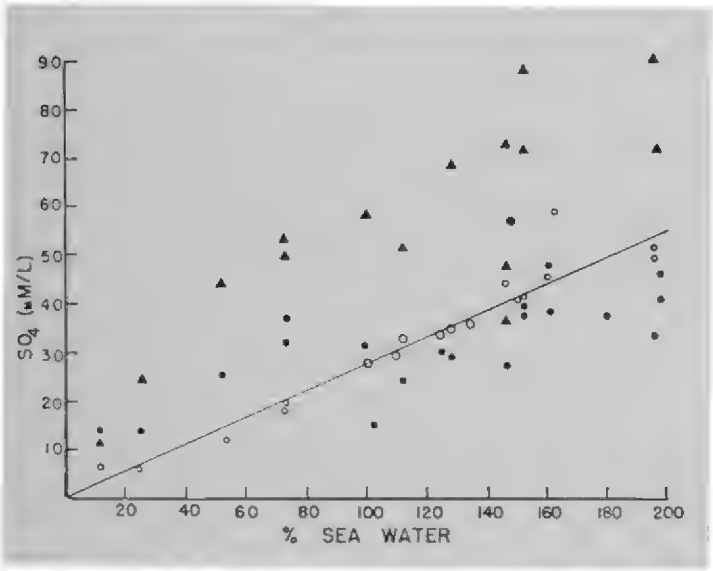

FIG. 10. Chloride concentrations of blood (dots), urine (triangles), and medium (circles) of *Ocypode*, plotted against sea water concentrations.

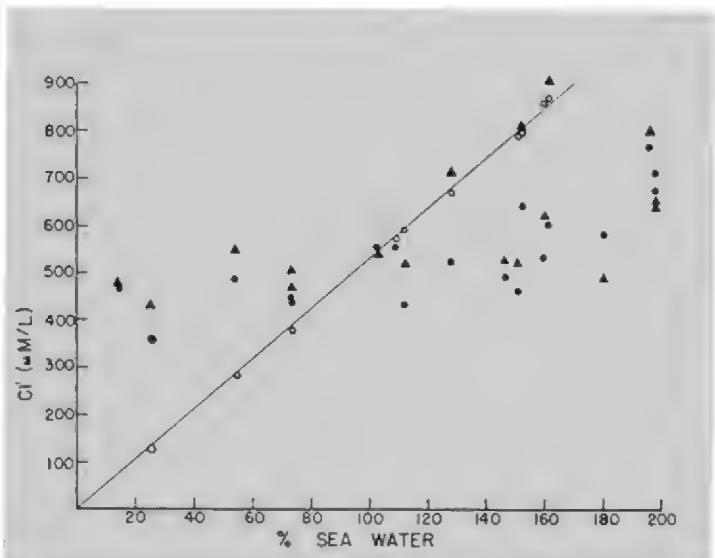

FIG. 11. Sulphate concentrations of blood (dots), urine (triangles), and medium (circles) of *Ocypode*, plotted against sea water concentrations.

At low temperatures, the U/B ratio is near unity at all salinities. At high temperature, it is near unity at low salinities, but increases at high salinities. At high temperature and high salinity where urine Na is reduced, the urine Cl concentration is high. This indicates that Na and Cl ions are excreted by separate routes under these conditions.

Blood SO_4 is less well-regulated and is subject to greater relative variation at all salinities (Fig. 11) than any of the other ions studied. Variations in blood $SO_4 =$ are correlated to some extent with temperature, but differences between the high and low temperature groups are not striking.

The poor regulation of blood SO_4 is not consistent with the regular increase in urine SO_4 as salinity rises. Sulphate is higher, with one exception, in urine than in medium or in blood at all salinities. The ratios of concentrations of Mg to SO_4 in urine are given in Table 3. Urine Mg/SO_4 ratios are between 0.82 and 1.12 for seven out of 19 animals. For the remaining 12 animals, the ratios range outside these limits from 0.52 to 2.37. This indicates that Mg^{++} and $SO_4 =$ are not necessarily excreted together. Urine Mg is generally lower than urine SO_4 at low salinities (below 73% S.W.), and higher at high salinities. Temperature has no apparent effect on the relative concentration of the two ions.

TABLE 3

Ratios of concentrations of Mg to SO_4 in urine of *Ocypode* at various salinities

Percent sea water	12–25°C	29–30°C
14	2.37	.....
25	.....	0.83
55	0.85	.....
73	.....	0.52
103	1.4	.....
109	.....	0.93
112	.....	1.12
128	.....	1.64
146	1.24	.....
146	1.01	.....
146	1.62	.....
146	1.28	.....
151	.....	1.37
152	.....	0.92
160	.....	2.06
196	1.42	.....
197	1.40	.....
197	1.40	.....

The ratio of total equivalents of anions to cation (Table 4) is useful in consideration of each of the three classes of fluids tested. For sea water, since Na, K, Ca, Mg, Cl, and SO_4 constitute over 99% of the ions present, the ratio can be used as a check on analytical accuracy. For blood and urine, the ratio can be used to detect the presence of charged solutes not included in the analyses.

The ratios for sea water included in Table 4 average 1.005 ± .026. Most of the individual analyses checked fairly well with tables of the ionic composition of sea water (Barnes, 1954), even though the samples were taken near shore.

TABLE 4

Electrical balance ratio (total mEq/l of anions to total mEq/l of cations) in blood, medium, and urine of *Ocypode* in different sea water concentrations. A positive ratio indicates a cation deficit.

Percent S.W.	Temp.	Urine		Blood		Media
		12–25°C	29–35°C	12–25°C	29–35°C	
14	20	1.29	.....	1.039	.....	.....
25	30	.....	6.30	.....	0.867	1.012
55	25	1.35	.....	0.873	.....	1.078
73	30	.....	2.45	.....	0.833	0.994
73	25	1.165	.....	0.857	.....	1.001
103	15–20	1.185	.....	0.949	.....	0.995
109	30	.....	1.29	.....	1.005	1.00
112	29	.....	1.69	.....	0.830	0.973
128	31	.....	1.73	.....	0.962	1.030
146	15–20	0.983	.....	0.975	.....	1.00
146	15–20	1.08	.....	0.984	.....	.....
146	15–20	0.935	.....	1.013	.....	.....
146	15–20	2.6	.....	0.978	.....	.....
151	29	.....	1.52	.....	0.940	0.996
152	30	.....	2.72	.....	0.962	0.990
160	29	.....	1.61	.....	0.920	1.001
161	35	.....	.....	.....	0.843	1.003
196	12	1.23	.....	1.048	.....	0.984
197	15–20	0.913	.....	0.969	.....	1.004
197	15–20	1.5	.....	1.000	.....	1.004
Averages:		1.29		0.962	0.906	1.005 ± 0.026

The ratios for blood are usually less than unity, that is, there is a cationic excess. Precision of analysis was lower for blood than for either urine or sea water. This may have been due to the relative difficulty of measuring small samples because of viscosity or to interference by organic constituents of the blood. Blood ratios are classified according to the temperature at which sampling was done. The average of the low temperature group was 0.962; of the high temperature group, 0.903. This indicates that between 4 and 10% of the negative charge of the blood is carried by substances not analyzed. This difference may be attributed to some other ion, but it is not probable. It seems more likely that at the pH of blood (near 7), the proteins are negatively charged to this extent.

In urine, on the other hand, the ratio $-/+$ is nearly always greater than unity, that is, there is an anionic excess. The deviations are much larger than in the blood, and rations for urine in the high temperature range are between 1.29 and 6.3 (the latter value being at lowest salinity), and average 2.45. The average may be high because of a few high values. The ratios for the low temperature group range between 0.913 and 2.6, averaging 1.29. These correspond to the distribution of high and low urine Na values. At low temperatures urine Na is much higher than at high temperatures, and the amount of undetermined cation necessary to maintain electrical neutrality is reduced. In *Uca,* where a similar cationic deficit occurs in the urine, it is largely made up by ammonia (Green et al., 1956, 1959). It is possible that ammonia is an important cation in *Ocypode.*

In December, 1956, an experiment was performed to determine the role of the gut in ionic regulation. Animal mortality due to cold prevented completion of the experiment, but samples of blood, urine, stomach fluid and medium were obtained from four crabs living in 146± S.W. and one in 103% S.W., at 15–20°C. Results of analyses of stomach fluids are presented in Table 5. Two types of stomach fluid were obtained. One, drawn from just inside the mouth, was clear and did not foam. It contained little protein (0.5%), and resembled water in its viscosity and surface tension. The other, drawn from deep in the stomach, was clear and yellow. It foamed easily, contained more protein (12–13%), and spread in a thin film on paraffin. It was the only type obtained from crabs No. 1 and No. 2. Crab No. 3 gave only clear fluid, while crab No. 5 (in normal S.W.) gave both types. Crab No. 4 regurgitated its stomach contents, and an uncontaminated sample could not be obtained.

As shown in Table 5, concentrations of most ions in stomach fluid differed considerably from those in blood. Stomach fluid to blood ratios are given for each ion. In the high salinity crabs, all ions are more concentrated in stomach fluid than in blood, but the stomach fluid to blood ratios vary between ions. The average ratios are highest (between 2 and 3) for K, Mg, and SO_4 but lower (1–2) for Na, Ca, and Cl. For individual crabs the ratios for Mg and SO_4 are similar, as are the ratios for Na and Cl. All ions are more concentrated in stomach fluid than in urine.

This indicates that the digestive tract may play a part in blood regulation by these crabs in high salinity. Osmotic concentrations were not measured, but S.F./B ratios for summated moles of analyzed ions in crabs No. 1, No. 2, and No. 3 were 1.27, 1.32, and 1.29, respectively. In crab No. 5, total molar S.F./B ratios for the clear and yellow stomach fluids were 1.33 and 1.45, respectively. An osmotic gradient across the stomach wall is indicated.

TABLE 5

Ocypode stomach fluid analyses. All values are in mM/l.
Crabs 1–4 in 146% S.W. *Crab #5 in 103% S.W.

Ion	Crab number	Urine	Blood (B)	Stomach fluid (S.F.)	S.F./B	Medium
Na	1	538	561	604	1.08	675
	2	457	519	686	1.32	
	3	450	429	596	1.39	
	4	44	461	..		
	*5	402	335	410/	1.22	433
				/435	1.30	
K	1	13.1	9.2	15.3	1.66	13.5
	2	14.9	6.6	18	2.73	
	3	11.5	6.8	19.2	2.83	
	4	12.7	6.0	.....	... .	
	*5	13.9	5.8	11.5/	1.98	8.8
				/8.4	1.45	
Ca	1	11.7	12.4	20	1.61	13.7
	2	11.1	12.8	12.2	0.96	
	3	12.5	10.9	13.4	1.23	
	4	5.3	12.2	..	... .	
	*5	9.6	10.2	11.3/	1.11	10.2
				/15.4	1.51	
Mg	1	59.4	34	125	3.71	71.5
	2	49	30.2	78.2	2.59	
	3	62.5	32.0	69	2.16	
	4	94	32.5	..	.....	
	*5	43	22.2	48/	2.11	52.5
				/75	3.38	
Cl	1	585	590	707	1.20	769
	2	543	555	742	1.34	
	3	496	473	678	1.43	
	4	518	486	.	. .	
	*5	.....	358	475/	1.33	540
				/471	1.31	
SO_4	1	47.9	27.7	93	3.36	44.7
	2	48.3	26.8	60.2	2.25	
	3	37.3	28.1	60	2.13	
	4	73.2	28.2	..	.....	
	*5	31.4	15.4	78	5.06	27.8

* In each crab no. 5 the upper value for stomach fluid is for fluid from the esophagus, the lower value is for fluid from deep within the stomach.

The relative concentration of ions in stomach fluid differs considerably from sea water. These results suggest that K and SO_4 are more concentrated in gut fluid than in sea water, while Na and Cl are less and Ca and Mg are variable.

Absorption of unchanged sea water through the stomach wall and excretion of the contained salts in the urine appears unlikely, as does selective absorption of water alone. The relationship between gut and blood is too complex to be clarified by these few measurements, but they suggest some passage of Na and Cl from gut fluid into blood, and net movements of K, SO_4, Mg, and Ca in the opposite direction.

Stomach fluid was also more concentrated than blood for all ions in the normal salinity crab. For all ions but SO4, the S.F./B ratios are similar to those for high salinity crabs. The one normal salinity S.F./B ratio for SO_4 is 5.06.

The normal salinity crab was hypo-regulating to about the same degree as the four high salinity crabs. Its summated molar B/M ratio was 0.68, while the ratios for the high salinity crabs were 0.78, 0.62, and 0.65, respectively. It appears that the gut of this normal salinity crab was also helping in blood regulation, especially the total concentration of SO_4, Mg, and K.

Although these preliminary observations were limited in number, they indicate that considerable ionic gradients are maintained across the stomach wall. All of the land crabs studied in this investigation excreted solid or semi-solid feces, indicating water reabsorption in the intestine. Since stomach fluid is more concentrated than blood, any such water absorption must be against a gradient. Complete analyses of feces are needed to clarify the role of the gut in blood regulation. In addition, regurgitation was sometimes noted and may serve to eliminate some salts.

Urine and blood of six *Ocypode* were sampled shortly after their capture on the beach. Traps on the beach near the laboratory were visited at hourly intervals during one day. When a crab was found in one of these traps, it was returned to the laboratory immediately, and urine and blood samples were taken. Three of the crabs were captured while they were running around on the beach, before they could return to their burrows.

Results of blood and urine analyses (Table 6) and comparison with measurements

TABLE 6

Concentrations of ions in blood and urine of fresh-caught *Ocypode*. All values in mM/l except protien.

	Crab	Na	K	Ca	Mg	Cl	SO_4	Protein percent
Urine	1	429	9.7	13.6	46.5	422	23.5	....
	2	345	10.5	14.0	25.0	472	10.4	....
	3	300	13.5	11.6	31.8	411	21.3	....
	4	357	5.3	12.5	29.2	448	24.0	....
	6	466	10.0	11.0	29.2	480	16.3	....
	Average	379	9.8	12.5	32.3	447	19.1	....
Blood	1	434	7.3	14.6	22.0	456	24.0	2.8
	2	489	6.7	16.2	31.0	506	27.9	6.2
	3	480	6.8	13.7	26.8	521	19.0	2.8
	4	429	6.1	16.0	27.5	452	25.0	6.6
	5	405	6.8	17.0	29.5	432	25.0	9.5
	6	456	8.3	16.5	35.0	484	21.7	....
	Average	449	7.0	15.7	28.6	475	24.1	5.6
	U/B of averages	0.84	1.40	0.79	1.13	0.94	0.79	....

made on crabs living in known salinities reveal the following:

1. Blood is slightly hypo-osmotic to normal sea water.

2. Urine is slightly hypo-osmotic to blood, and this is due to low Na, Ca, Cl, and SO_4 concentrations. Magnesium and potassium are slightly higher in urine than in blood.

3. Blood values for freshly collected crabs are similar to those found in crabs living in dilute sea water, except that blood Mg and SO_4 concentrations are lower than those measured in animals kept in dilute water in the laboratory. A very small (1%) cation deficit exists in the urine, while the blood has a larger (4%) anion deficit.

4. Freezing points were not measured, but summated concentrations of both cations and anions were lower in urine than in blood. This would seem to indicate a slight but definite hypo-osmotic urine, especially when the added effects of organic solutes on blood pressure are considered.

5. It would appear that in nature the antennary gland acts to conserve Na, Ca, SO_4, and possibly Cl while excreting K and Mg.

Relationship of Internal Medium to External Medium in *Cardisoma* and *Uca*

For comparison with *Ocypode* analyses were also made for two other terrestrial species, *Cardisoma guanhumi* and *Uca pugnax*, relative to hypersaline conditions.

Cardisoma guanhumi is a large, tropical land crab occasionally found along the south Texas coast. It is a member of the family Gecarcinidae in contrast to *Ocypode* and *Uca*, which are in the family Ocypodidae. Four *C. guanhumi* were obtained in September, 1956. Blood, urine, and medium samples were taken from one of these after three weeks exposure to 125% S.W. Temperature at the time of sampling was 17°C (Table 7).

Table 7

Analyses of blood, urine, and medium of *Cardisoma guanhumi* in 125% sea water.

	Na	K	Ca	Mg	Cl	SO_4
Urine	305	27.6	13.5	102	364	68
Blood	436	6.2	12.7	42.5	442	30.8
Medium	561	11.9	12.2	64	656	33.9

Uca pugnax were kept in 12 inch glass bowls containing about a centimeter of 100% S.W., for several days after capture. Ten crabs were kept in each bowl. The sea water concentration was gradually increased during five days to about 170% S.W. (900 mM Cl/1). After two days in this salinity, concentrations of Na, K, Cl and SO_4, as well as osmotic concentration, were determined for blood, urine and medium (Table 8). Temperatures during this period did not exceed 25°C. The concentrations of all ions and the osmotic concentration were much lower in the blood than in the medium. Urine Na concentration was much lower than that of blood or medium, and urine SO_4 much higher, but Cl was only slightly higher in urine than in blood. These results are in general agreement with findings of Green *et al.* (1959) for *U. pugnax* and *U. pugilator* at Woods Hole. Some extrarenal route of Na excretion is indicated.

Table 8

Determinations of ionic and osmolar concentrations (o.c.) in blood and urine of *Uca pugnax* acclimated to 170% S.W. All values are inmM/l except osmotic concentrations, which are in NaCl equivalents.

Ion	Medium	Blood	Urine	U/B	B/M
Na	714	455	140	0.31	0.64
K	15	11.5	22	1.91	0.77
Cl	893	537	546	1.02	0.60
SO_4	45.8	26.6	85.5	3.22	0.58
O.C.	0.889	0.548	0.613	1.19	0.63

That sodium might be excreted by the gills was tested on fluid drawn by capillary pipette from the gill-chamber opening between the last two legs. The fluid thus obtained was clear and watery. It did not clot in air or precipitate in concentrated salt solution. Samples were taken from six crabs which were living in water that had been allowed to evaporate to a concentration of 1140 mM Cl/1. Samples of this fluid and the medium were analyzed for sodium. The Na concentrations in mM/L were as follows: medium, 975; gill chamber fluid, 920, 840, 745, 735, 735, and 717.

Since this gill fluid did not clot, and no precipitate formed when it was added to concentrated salt solution, it is unlikely that the fluid was contaminated with blood. There was no indication of Na secretion into the gill chamber, but rather, Na concentration was lower than in the medium.

Effect of Temperature on Hypo-regularity Ability in *Uca*

The work on *Ocypode* and *Uca* in Texas described above suggested that temperature might affect regulatory ability, but the tests at different temperatures were not done simultaneously and temperatures were not controlled. A subsequent test of the effect of temperature on the regulatory ability of *Uca pugnax* was done at Urbana, Illinois, on animals imported from Woods Hole, Mass. The results, preesnted in Table 9 and in Fig. 12, show that under constant hypersaline stress blood and urine osmotic concentration and urine Na concentration vary considerably with temperature.

Magnesium Injection Experiments on *Ocypode* and *Uca*

Prosser *et al.* (1955) found that the decrease in urine Na in *Pachygrapsus* in high salinity could be abolished by placing the animals in artificially concentrated sea water lacking Mg. It was concluded that the shift in Na excretion was associated with Mg stress rather than hyper-osmotic stress.

Table 9

Urine and blood osmotic concentrations and urine Na concentrations of Uca in 190% sea water at 10, 21, and 30°C.

Temperature °C	Osmotic concentration (in NaCl equivalents)				Urine Na	
	Urine	n	Blood	n	(mM/l)	n
10	0.622 ± .038	18	0.554 ± .067	12	272	3
21	0.517 ± .032	12	0.480 ± .034	6	75	3
30	0.763 ± .078	12	0.730 ± .054	6	256	3

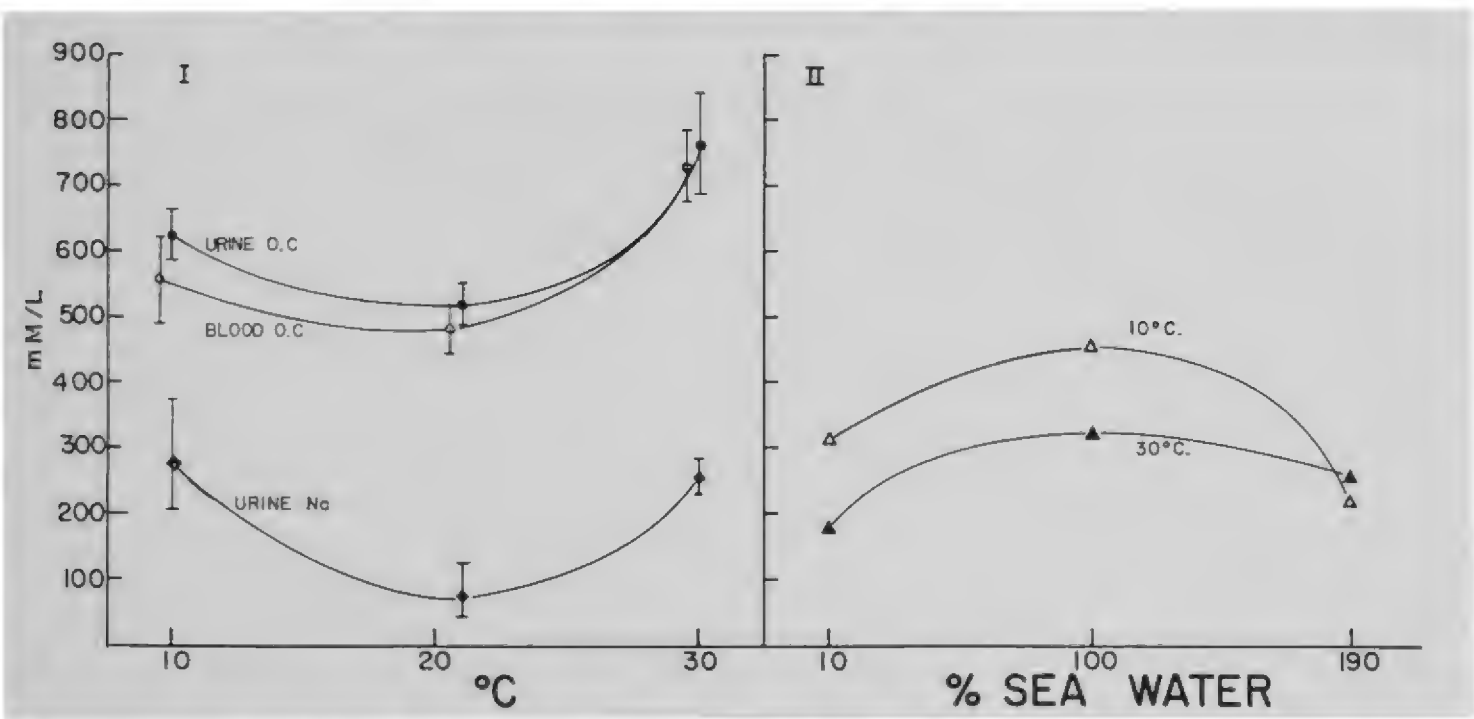

Fig. 12. (I) Upper lines represent osmotic concentrations of *Uca pugnax* blood (circles) and urine (dots) in 190% sea water at 10, 21, and 30° C. Lower line represents urine Na under the same circumstances. (II) *Uca pugnax* urine Na concentrations in various sea water concentrations at 10 and 30° C.

The corollary of this, that a change in urine Na might follow application of Mg stress without osmotic stress, was tested in *Ocypode* and *Uca* by injecting $MgCl_2$ into the haemocoele and measuring subsequent Na and Mg concentrations in urine. Because of the findings described above that urine Na in *Ocypode* was affected by both salinity and temperature, injections were done under different combinations of the two variables.

Fig. 13 shows that injection of $MgCl_2$ into crabs living in 100% S.W. at 23°C, where initial urine Na is high, is followed by decreased urine Na and increased urine Mg un-

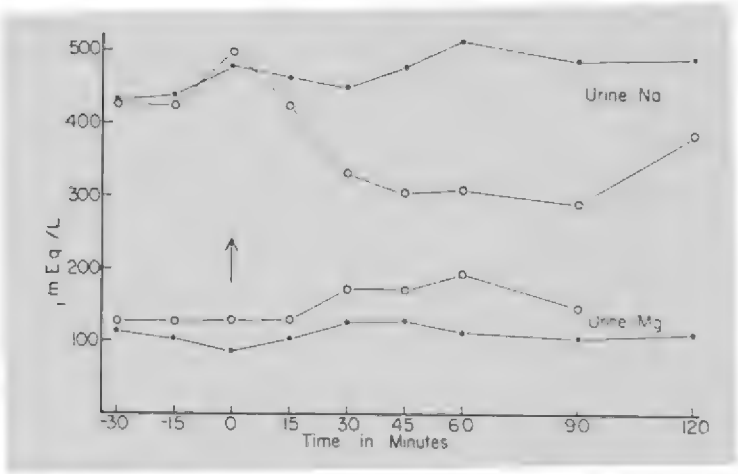

FIG. 13. Changes in urine Na and Mg levels in *Ocypode* living in 100% S.W. at 23° C following injection of 0.05 ml 60% S.W. (dots) and 0.05 ml 1 molar $MgCl_2$ (circles). Sodium values are averages from two crabs, Mg values are for one. Arrow indicates time of injection.

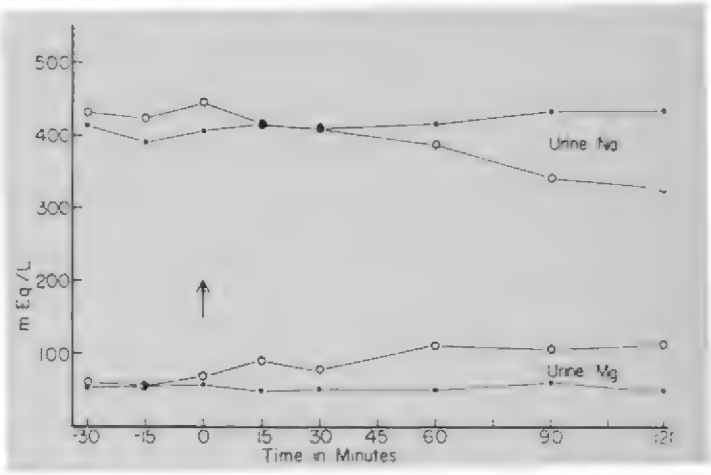

FIG. 14. Changes in urine Mg and Na concentrations in *Ocypode* living in 10% S.W. at 10–15° C following Mg injection. Dots represent average values for the non-injected and sea water injected controls. Circles represent values for the Mg injected experimental crab.

like the sequence in controls injected with sea water. Fig. 14 shows similar results for crabs living in 10% S.W. at 15–20°C, where initial urine Na is also high. Mg injection into a crab living in 10% S.W. at 25–30°C, where initial Na was low, was followed by an increase in urine Na (Gifford, 1958).

Similar experiments were done on *Uca* under more carefully controlled temperature conditions. The results, presented in Fig. 15, are similar to those with *Ocypode*. If urine Na is initially high, it decreases after Mg injection; if initially low, it increases. These changes do not occur in sea water injected or non-injected controls.

Comparison of Blue Crab Populations from a Hypersaline Environment with Populations from a Hyposaline Environment

In three experiments crabs were taken from the hypersaline Laguna Madre, from the low salinity Guadalupe River area, and from the waters near the Gulf at Port Aransas and acclimated to the same Gulf salinity conditions. Salinities were varied and tolerances and fluid contents of all crabs were studied. A comparison of the physical dimensions of *Callinectes sapidus* from the Laguna Madre with those reported from the low salinity Chesapeake Bay by Newcombe and Gray (1941) was made (Table 10), but only one morphological difference was demonstrated. Physiological differences, however, were found as indicated in Tables 14–19. Further details on individual crabs, sizes, and other data are given in the original dissertation (Gifford, 1958).

In the first experiment (May, 1956) tolerance of crabs to varying salinity from normal sea water and from high salinity was determined by comparing their ability to survive exposure to gradually increasing salinity (5 ‰ per day) after an initial period of 10–12 days acclimation to normal sea water. Blood, medium, and urine osmotic con-

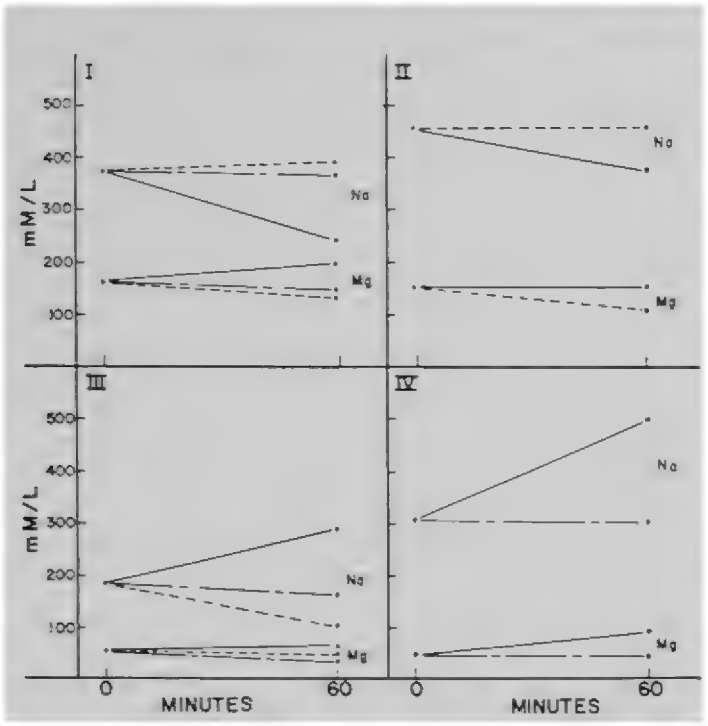

FIG. 15. Changes in urine Na and Mg concentration in uninjected (————), sea water injected (– – – – –) and $MgCl_2$ injected (——) *Uca pugnax* at various salinities and temperatures: I 100% sea water at 30° C, II 100% sea water at 10° C, III 10% sea water at 30° C, and IV 10% sea water at 10° C.

TABLE 10

Comparison of measured dimensions of *C. sapidus* from the Laguna Madre (1) with dimensions calculated by equations* from Chesapeake Bay (2). All values are in mm, and are averages for 10 crabs.

	1 Measured		2 Calculated		Difference (1–2)
	Average	Range	Average	Range	
Width	66.3	62.8–71.9	.....	.....	....
Length	32.2	30.6–34.7	31.8	30.4–34.2	0.4
ES	30.0	26.7–32.8	25.8	24.1–27.8	4.2
CJ	32.1	28.2–36.5	30.7	28.4–34.5	1.4

* Newcombe and Gray, 1941.
ES Distance from eye to lateral spine tip.
CJ Distance from claw tip to first joint.

centrations were measured (Table 11). Blue crabs from the Laguna withstood higher salinities than those from the open bay and Gulf. All control crabs survived transfers to low salinity (22 ‰) in this experiment.

In the second experiment during August and September, 1956, the acclimation period was extended and large abrupt salinity stresses in both directions were applied. Blood

TABLE 11

Survival time of *Callinectes sapidus* gradually transferred into high salinities

	No. of crabs	Survival time in hr
Controls*	7	240+
Crabs from Laguna Madre at 38‰ into 58‰	10	24, 118, 192, 24, 96, 96 192+, 192+
Crabs from Port Aransas channel at 32–40‰ into 48‰	5	<24

* 2 channel crabs and 5 Laguna crabs transferred into low salinity and observed beyond 200 hr.

and media were analyzed for major inorganic constitutents at various intervals following application of stress (Table 12). Twelve male and nine immature female *C. sapidus* caught in the Laguna Madre were subjected to gradual reduction in salinity. Water was changed every three days; the crabs were fed fish once a week. Twelve large male crabs were obtained from the Guadalupe River at 13 ‰. Both groups were kept in normal sea water at 25–30°C. Transfers to other salinities were made in three parts, after from 8 to 32 days acclimation at 38 ‰.

In part 1, the upper lethal salinity limit for *C. sapidus* from the Laguna Madre was determined. One Laguna crab was moved abruptly from 38 to 62 ‰. It showed no ill effects after 96 hours, and was returned to 100% seawater. Next, eight Laguna crabs (2 or 3 to a bowl) were moved abruptly from 38 to 62 ‰. Two were killed by the others. After 96 hours, the six survivors were transferred to 72 ‰. Three of these died within 48 hours. After 72 hours at 72 ‰, the remaining three were transferred to 87 ‰. One of these died within 24 hours, and the last two within 48 hours. Blood and medium samples from one of these crabs after 24 hours at 87 ‰ (Cl = 1420 mM/L) are included in Table 12 as "Crab 1".

In part 2 low salinity tolerances of Laguna and river blue crabs were compared. Five Laguna crabs and two river crabs were used. All survived for 48 hours after abrupt transfer to 25% S.W. (9 ‰, Cl = 150 mM/L). Further abrupt salinity reduction to 5% S.W. (1.5 ‰, 28.6 mM Cl/L) resulted in the death of one Laguna crab in six hours and the other four within 21 hours. Of two river crabs tested, one died between 48 and 72 hours, and the other lived 144 hours and was returned to S.W. Blood and medium samples were taken for this crab at 96 hours ("Crab 2," Table 12).

In part 3, high salinity tolerances of Laguna and river blue crabs were compared. After at least 10 days acclimitization at 38 ‰, eight Laguna crabs and four river crabs were transferred to 60 ‰ (Cl = 1050 mM/L). The four river crabs died at 26, 60, 72 and 79 hours exposure, while one Laguna crab died at 60 hours and the other seven lived for 120 hours and were returned to 100% S.W. Analyses of blood and medium samples taken from the moribund river crab and the active Laguna crab at 79 hours are presented in Table 12 as "Crab 3" and "Crab 4," respectively.

In the third experiment an extended, three month, acclimation period was attempted before exposure to high salinity. In September, 1956, 24 river crabs (captured in 13 ‰)

TABLE 12

Analyses of blood and medium samples collected during second blue crab experiment. All values are in mM/l.

Crab	Fluid	Na	K	Ca	Mg	Cl	SO_4	Total molar conc.
1*	Blood	774	14.6	17.5	52.5	894	15.5	1768
	Medium	1225	40	22	128	1420	69.5	2935
2†	Blood	161	6.9	3.2	12.5	188	6.1	378
	Medium	23	0.8	0.5	2.1	27.1	0.7	54
3‡	Blood	666	15.0	11.4	46	722	8.6	1469
	Medium	899	20.1	19.4	102	1041	52	2134
4§	Blood	688	13.5	11.9	58.5	780	11.1	1563
	Medium	968	21.6	20.6	110	1118	54	2477

* Laguna crab sampled after 24 hours in medium shown and 120 hours in (Cl) more than 970 mM/l.
† River crab after 96 hours in medium shown.
‡ River crab after 79 hours in medium shown.
§ Laguna crab after 79 hours in medium shown. Media for crabs 3 and 4 were separately prepared by dilution from a concentrated stock solution.

and 29 Laguna crabs (captured in 51 ‰) were transferred to tanks of normal sea water (36–38 ‰). Fourteen of the river crabs died within 36 hours, seven of the remaining 10 were still alive in December and were used in this experiment. There was no immediate mortality among the Laguna crabs, but all of them were dead in December and an attempt was made to capture more Laguna crabs to replace them. Crabs were very scarce in the Laguna at that time, and survival in the laboratory was poor, even among crabs kept in dishes of the water in which they had been captured. Analyses of body fluids and media sampled at the time of capture of some of these crabs (Table 13) showed that

TABLE 13

Results of analyses of body fluids and media during winter (Dec. 1956) for Laguna Madre *C. sapidus* sampled immediately after capture. All values in mM/l.

Crab	Fluid	Na	K	Ca	Mg	Cl	SO_4	Total molar conc.
1	B	704	14.9	15.9	55.3	782	16.0	1578
	M	790	16.1	22.0	80	925	46.6	1880
	B/M	0.89	0.93	0.72	0.69	0.85	0.34	.....
2	B	614	14.4	14.0	52.5	611	10.8	1316
	M	735	16.5	13.9	68.9	815	40.2	1690
	B/M	0.84	0.87	1.01	0.76	0.75	0.27	.....
3	B	529	10.9	10.0	39	612	11.2	1212
4	B	524	9.2	9.8	37	608	11.8	1200
5	B	485	13.1	11.6	35	618	14.1	1212
	M	608	11.4	12.1	67	690	35.5	1399
	B/M	0.84	0.97	0.85	0.55	0.89	0.28	0.86
6	M	782	15.8	20.2	88	894	46.2	1845
	U	838	15.4	15.4	48.4	829	26	1773
	B	786	16.4	16.9	53.0	814	11.9	1698
	B/M	1.0	1.04	0.84	0.60	0.91	0.26	.....
7	U	822	17.8	25.4	87.5	.....	.....	.....
	B	802	18.6	20.0	56.0	911	9.7	1817
	C Fl	863	14.4	30.5	120	968	89.3	2085
	B/M	1.03	1.18	0.99	0.64	1.02	0.21	.....

five out of seven were regulating all ions to some extent. Magnesium, and especially SO_4, were well regulated in all of them.

Seven Laguna crabs were brought gradually to normal sea water and were held there with the seven river crabs for a one week control period. Blood and medium chloride concentrations at the beginning and end of this period are given in Table 14. All crabs were then transferred to hypersaline water (61 ‰). Survival times (Table 15) were much shorter among the Laguna crabs, three of which were killed during fluid sampling. Analyses of body fluids of these crabs at various times after application of hyper-saline stress (Table 16) show that while there were differences in the rates of increase of blood

TABLE 14

Mean chloride concentrations in mM/l of crab blood and medium during the control period of the third blue crab experiment. The number of individuals is indicated in parentheses

		Blood	
Date	Sea water	River crabs*	Laguna crabs†
12/22/56	533	519 (7)	551 (6)
12/27/56	543	531 (6)	552 (4)

* Collected at 13‰ and acclimated three months at 38‰.
† Collected at 43–58‰ and gradually transferred to 38‰.

TABLE 15

Survival time of *Callinectes sapidus* transferred from 38‰ into hypersaline water, 61‰

	No. of crabs	Survival time (hr.)
Guadalupe River crabs*	7	100 to 230
Laguna Madre crabs†	8	48‡, 12, 22, 48, 48, 96‡, 112‡

* Collected at 13‰ and acclimated three months at 38‰.
† Collected at 43–58‰ and acclimated one week at 38‰.
‡ Three killed drawing gut fluid.

TABLE 16

Average concentration of ion in media and body fluids of *Callinectes sapidus* from the Guadalupe River* and Laguna Madre† under hypersaline stress of transfer from 38‰ into 61‰ (at 0 time). Concentrations are in mM/l.

Group	No. of crabs	Time hr.	Na	K	Ca	Mg	Cl	SO_4	Total molar conc.
MEDIA	..	0	470	9.9	10.2	53.5	544	28.0	1116
	..	168	865	18.6	18.5	98	1033	51.5	2056
BLOOD									
River	5	0	456	9.2	13.7	37.5	515	7.3	1039
	1	26	598	13.3	19.4	51.5	681	19.1	1362
	1	62	634	10.3	14.7	56.7	710	13.1	1439
	4	168	830	19.3	21.9	74.8	940	23.2	1909
Laguna	3	0	484	8.1	13.1	41.2	588	8.7	1143
	1	27	726	14.8	20.4	60.0	843	13.5	1678
	1	55	792	10.2	20.8	58.0	920	11.6	1812
	1	96	922	19.6	21.6	61.0	1002	24.4	2074
	1	192	863	20.6	21.2	66.0	938	20.3	1929
RATIO OF BLOOD TO MEDIUM									
River	4	168	0.96	1.04	1.12	0.76	0.94	0.45	0.93
Laguna	1	192	1.00	1.16	1.08	0.67	0.94	0.39	0.94
URINE									
River	5	0	470	10.1	12.9	39.3	530	32.3	1100
	1	26	646	16.2	21.4	52.0	720	46.6	1502
	1	62	690	17.4	22.6	79.8	690	67.5	1567
	4	168	808	22.5	26.5	90.5	912	84.6	1944
Laguna	3	0	521	9.1	16.1	49.9	544	60.9	1202
	1	27	728	13.3	27.2	104	826	77.5	1776
	1	55	844	16.3	26.4	80.5	936	82.5	1986
	1	96	831	17	23.9	108	903	93.0	1976
	1	192	832	26.1	25.2	122	925	96.2	2027
RATIO OF URINE TO BLOOD									
River	4	168	0.97	1.17	1.21	1.21	0.97	3.65	1.02
Laguna	1	192	0.96	1.27	1.19	1.85	0.99	4.74	1.05
STOMACH FLUID									
River	2	0	520	11.6	12.0	44.7	566	21.1	1175
	1	26	724	14.7	15.8	76.5	815	37.8	1684
	1	62	687	11.9	22.8	101	872	33.2	1611
	4	168	842	19.0	22.0	108	962	45.0	1998
Laguna	1	0	507	9.3	11.4	45.0	546	32.1	1151
	1	55	892	10.8	20.4	68.5	935	31.5	1958
RATIO OF STOMACH FLUID TO BLOOD									
River	4	168	1.01	1.01	1.04	1.64	1.02	1.94	1.05
	1	55	1.13	0.94	0.98	1.18	0.98	2.71	0.925

* Collected at 13‰ and acclimated three months at 38‰.
† Collected at 43–58‰ and acclimated one week at 38‰.

concentrations between the two groups, bloods of the four river crabs and one Laguna crab which survived 7 or 8 days were nearly identical. Sulphate, and to a lesser extent, magnesium, were the only ions being regulated. Concentrations of these ions were higher in stomach fluid and urine than in blood.

Discussion

The results of this work support the findings cited in the introduction that both semi-terrestrial and certain estuarine crabs are capable of hypo-osmotic regulation. *Ocypode* and *Uca* on one hand, and *Callinectes* on the other, are similar in that they can all withstand both high and low salinity stress for long periods, but they differ in the mechanisms used.

The blue crab occurs naturally in waters where salinities of 58 ‰ (150% S.W.) may persist for months. It lives immersed, and gill ventilation and stress are more or less continuous. It accomplishes this by allowing blood concentrations of Na, K, and Cl (and presumably osmotic concentration) to rise (B/M ratios vary between 0.7 and 1), while blood concentrations of Mg, and to a greater extent, SO_4, are held down (B/M ratios of 0.5–0.7, and 0.2–0.3, respectively) at least in part by excretion in the urine and concentration in the stomach fluid. Response to application of even greater stress in the laboratory was similar, for Laguna crabs, although duration of stress was only 3–7 days. In one case (Table 5, crab No. 1) a Laguna crab was alive and active with blood concentrations of the major ions about equal to their concentrations in 150% S.W.

In *Uca* and *ocypode* response to high salinity stress differs from that of *Callinectes* in that blood Na, K, Mg, and Cl, and probably as a consequence, blood osmotic concentrations, are well regulated (B/M ratios from 0.4–0.7) while Ca and SO_4 are not regulated as well as they are in *Callinectes*. Although intracellular electrolyte concentrations have not been studied in any of these species, it would seem that *Uca* and *Ocypode* do most of their regulating at the boundary between blood and medium, while *Calcinectes* maintains lower gradients at this boundary and either maintains another series of gradients between blood and cells or tolerates large fluctuations in intracellular concentrations. Studies of the type done by Shaw (1955b) on fluctuations in concentrations of intracellular electrolytes in *Carcinus* might very profitably be extended to *Callinectes*, which has a wider range of blood concentrations. Such studies might provide information about both the activity of cell membranes in ionic regulation and about the effects of fluctuations of intracellular electrolytes on cell function.

In *Pachygrapsus* (Prosser *et al.*, 1955) the degree of regulation of various ions (expressed as per cent change from blood concentrations in 100% S.W.) varies with the direction of the applied stress (Table 17). This also appears true of *Ocypode*, *Callinectes* and *Palaemon serratus*. In *Callinectes* the order of decreasing regulation is exactly reversed on going from dilute to concentrated sea water. The two studies on *Pachygrapsus* (Prosser *et al.*, 1955; Gross, 1959) agree as to the order of decreasing regulation in dilute water, and except for Na, also agree in concentrated water. Difference in degree of regulation might be due to the manner in which stress was applied. There is no agreement, either as to order or as to degree, between the three species. This variation in *Pachygrapsus* was interpreted by Prosser *et al.* as showing that hypo and hyper regulation are fundamentally two different processes. An extension of this deduction is

TABLE 17

Regulation of ions in crabs during transfer into concentrated and dilute sea water. Values are per cent change from blood concentrations.

Species	Into dilute sea water							Into concentrated sea water						
	Per cent S.W.	Na	K	Ca	Mg	Cl	SO_4	Per cent S.W.	Na	K	Ca	Mg	Cl	SO_4
*Pachygrapsus**	50	—33	—31	—25	—70	....	....	170	44	44	8	13	..	..
Ocypode	14	—16	—10	—20	—23	—15	— 7	190	28	84	69	186	19	190
Ocypode†	50	—18	—10	—18	—32	....	....	150	21	38	23	36	..	..
Callinectes	5	—65	—25	—77	—33	—64	—17	185	82	111	60	99	83	218
Paleomonetes‡	50	—40	—13	+12	—12	—30	—56	120	20	33	19	64	15	23

* Prosser et al., 1955.
† Gross, 1959.
‡ Parry, 1954.

that ionic regulation depends on separate transport systems which either are not reversible or which do not work with equal efficiency in both directions.

Examination of the internal vs. external concentration curves for the different ions reveals that they cross the isotonic line at different points. In *Ocypode*, as external concentration increases, K and Mg regulation reverse at 60% S.W. Osmotic and total molar concentrations, Na (at 12–25°C), Cl, SO_4 regulation reverse at around 100% S.W.; Na (at 29–35°C) reverses at 110% S.W.; and Ca regulation does not reverse until external concentration reaches 180% S.W. It would seem that the concentration of each ion, or at least group of ions, is controlled separately, and that the different ion pumps can be running in different directions at the same time.

In spite of this variation in the handling of various ions, the ratio of total anions to total cations seems to be relatively constant for a number of Decapod crustaceans. Values calculated from blood analyses of several kinds of Decapods are presented in Table 18. Six of the twelve values fall between 0.958 and 0.963, agreement within 0.5%. All of the values outside of this range are for animals that were maintaining large ionic

TABLE 18

Ratios of constituents of bloods of marine Decapods in dilute, normal, and concentrated sea water

Species	No. of individuals	Per cent sea water	Ratio of anions* to cations* and standard deviations	Cl*/Na* and standard deviations	Ratio of osmotic concentration† to total molar concentration‡
Six Decapods (Prosser et al., 1950)	6	100	0.958 ± 0.020	1.091 ± 0.017	....
Palaemon serratus§ (Parry, 1954)	....	50	0.963	1.165	....
	8–20	100	0.963	1.091	....
	20	120	0.916	1.141	....
Callinectes sapidus	20	5–258	0.961 ± 0.051	1.131 ± 0.041	....
Ocypode albicans					
12–25°C	11–12	14–197	0.962 ± 0.041	1.078 ± 0.082	....
29–35°C	9	25–161	0.907 ± 0.057	0.963 ± 0.065	1.058 ± 0.106
After capture	6	100	0.961 ± 0.019	1.058 ± 0.015	....
15–20°C	5	103–146	0.983 ± 0.020	1.069 ± 0.019	....
Cardisoma guanhumi	1	125	0.911	1.011	....
Uca pugnax & puglicator (Green et al., 1959)	....	100	1.290	1.637	0.994 .....
	....	175	1.23	1.53	0.940 .....

* Total milliequivalents per liter.
† Osmotic concentration expressed in equivalents of NaCl as mM/l.
‡ Total of the solutes determined expressed in mM/l.
§ Calculated from mean ion concentrations.

and osmotic gradients under hypersaline stress; in the case of *Ocypode* combined with high temperature stress. In the cases where deviation occurs the ratio of anions to cations generally decreases; that is, the usual anion deficit becomes greater. *Uca* is exceptional in having an anion surplus instead of a deficit. Variation in the ratio Cl/Na parallels that for anions to cations. Chloride is relatively less concentrated in blood than in sea water (where Cl/Na is near 1,164), although in absolute concentration there is still more chloride than sodium.

There are several ways that the electrical balance may deviate from unity such as with undetected solute (anionic in all but *Uca*) with blood proteins carrying an electrical charge at blood pH, or with the binding of ions in undissociated complexes. Changes in the ratio may occur with addition of unidentified solute, or by change in blood pH.

One way of detecting unidentified solutes in the blood is by comparing osmotic concentration (O.C.) with total molar concentration (T.M.C.) of determined solute. Rarely are all the necessary measurements made on one animal. In the case of *Ocypode* at 29–35°C the average ratio O.C./T.M.C. for nine animals is 1.106, indicating that about 10% of the solute is not identified. The ratio of anions to cations averages 0.907, indicating that 9% of the anions have not been identified. The presence of undetected anionic solute seems likely. In *Uca* (Green *et al.*, 1959) the ratio O.C./T.M.C. is less than one, indicating that some of the solute is not osmotically active. Since there is an excess of anions, it may be that some of them are normally bound, either to proteins or in unionized complexes. The way in which these deviations are connected to hypo-ionic regulation is still unknown.

Several semi-terrestrial crabs, but not *Callinectes* or *Palaemon* (Parry, 1954), have been found to have low urine Na concentrations. The conditions under which this occurs are not always identical between species. This decrease in urine Na was first observed in *Pachygrapsus* (Prosses *et al.*, 1955), and confirmed for that species by Gross (1959). It does not occur in low salinity, and can be reduced or abolished by removing Mg stress. In *Ocypode* it occurs at all salinities at high temperature, but only in high salinities at low temperature. In *Cardisoma* it was found in one crab tested in 125% S.W.

In *Uca,* (Green *et al.*, 1959 and this paper) the decrease in urine Na is generally more pronounced and more consistent than in the other species. It occurs in both high and low salinities at all temperatures, and is minimal at intermediate salinities. In both *Uca* and *Ocypode* injections of small amounts (30–50 micromoles) of Mg into the haemocoele are followed by temporary fluctuations in urine Na and Mg concentrations. The direction of the change in urine Na depends on its preinjection concentration, which in turn is a function of both salinity and temperature. The changes in urine Na and Mg (in milliequivalents per liter) are not equal. It would seem that Mg excretion inhibits Na movements in the antennary gland. That this is not the only cause of the decrease in urine Na, at least in *Ocypode,* is indicated by data presented in Table 19. All combinations of high and low urine Na and Mg can occur. The high anion to cation ratios indicate large amounts of undetermined cations in the urine. The role of this shift in Na excretion in blood regulation is still unresolved. In *Uca,* Green *et al.* found that urinary NH_3, although high, did not completely make up the urine cation deficit. It may be that high temperature increases production of some cationic metabolite which is excreted in the urine at the expense of Na excretion.

It was shown by Flemister (1958) that urine production by *Ocypode* stops when water is unavailable. This was confirmed in this work by continuous withdrawal of urine

TABLE 19

Sodium (Na) and magnesium (Mg) concentrations in mM/l in blood (B) and Urine (U) of *Ocypode* under various conditions of salinity and temperature

Cl in medium	Temp. °C	Na	Mg	Ratio of anions to cations
72	17	U 433	27.5	1.29
		B 448	25.3	1.04
129	30	U 26	20.5	6.3
		B 346	36.3	0.867
840	29	U 83	184	1.61
		B 534	50.8	0.920
1036	17	U 620	103	0.913
		B 662	64	0.969

from crabs in air. After initial drainage of the bladders and one hour exposure to air, *Ocypode* produces urine at rates between 10 and 40% of body weight per day. At two hours the rate is around 5% body wt per day, and by three hours urine formation generally stops. Crabs kept in air apparently form urine until the bladders are full and then keep it, for urine can usually be obtained from crabs kept as long as forty-eight hours in air. Exchange of harmful metabolites and Mg for the sodium in stored urine may be of adaptive value and does not conflict with the available data, but there is no proof for such a mechanism.

Blood and urine samples taken from five ghost crabs captured on the beach (in December at 20°C) differed from those taken from crabs kept in the laboratory. Urine concentrations of all ions but Mg were lower than blood concentrations, and even for Mg the difference was not great. The ratios of total mM/L of determined solute in urine to total mM/L in blood averaged 0.878 ± 0.102. The urines contained from 12 to 338 mM/L fewer mM/L than did the bloods (avg. 137 ± 123). Salt conservation by production of hypotonic urine was unnecessary and ineffective, because urine production had supposedly stopped. Bladder volume is small compared to blood volume, and other routes of salt loss (except in feces) had been cut off. Although osmotic concentrations were not measured in these crabs, *Ocypode* kept in the laboratory had not demonstrated the ability to produce hypo-osmotic urine. Anion to cation ratios in the urines averaged near one, but the separate values were either below 0.92 or above 1.11. In order to be iso-osmotic to blood these urines would have had to contain from 12 to 338 mM/L of unidentified solute, which from the electrical balance figures could have been either anions or cations.

The effect of temperature on hyporegulatory ability was found to be of considerable importance in both *Uca* and *Ocypode*. At 25°C or less, *Ocypode* survived for at least three weeks in 180% S.W., and blood osmostic concentration after ten days exposure was only a few per cent higher than 100% S.W. Blood concentrations rose somewhat in 197% S.W., but the crabs survived for 7–10 days. At temperatures between 29 and 35°C blood concentrations rose in all concentrated media, and the crabs only survived 4 to 5 days in 160% S.W. Controlled temperature experiments with *Uca* indicate that blood osmotic concentrations (under equal hyper-saline stress) are better regulated at 21°C than at 10°C, and least regulated at 30°C.

Neither species (*Ocypode* from Texas or *Uca* from Woods Hole) withstood combined high salinity and high temperature. *Ocypode* retreated to its burrow, often with the entrance plugged, during the day in summer and during prolonged cold spells in winter. It was active during daylight at intermediate temperatures.

The effect of temperature on salinity tolerance of *C. sapidus* from the Laguna Madre was not clear. The literature on the effect of temperature on several euryhaline Crustacea has been summarized by Kinne and Rotthauwe (1952) and by Verwey (1958). In the crab *Eriocheir*, the amphipod *Gammarus*, and the prawn *Palaemonetes*, high temperature appears to reduce regulatory ability. This has been shown in this paper to be true of *Ocypode* and *Uca*. Many estuarine forms migrate to the sea in winter, among them peneid shrimp (Gunter, 1950) from the coastal bays of Texas. *Callinectes sapidus*, on the other hand, has been reported to migrate from Texas coastal bays to the open Gulf in summer (Daugherty, 1952). Simmons (1957) found that the number of species in the Laguna Madre was lower in summer than in winter. Simmons also reported that the numbers of *C. sapidus* found in the Laguna increased in winter when salinity was low, but this was not true in December, 1956, when salinity was high. The following observations by the writer indicate that *C. sapidus* differs from the Crustacea listed by Kinne and Rotthauwe (1952) with regard to salinity tolerance at high temperature:

1. Occurrence of *C. sapidus* in Aransas Bay during the spring and summer of 1956 followed the pattern reported by Daugherty (1952). They were abundant there in May when salinity was about 32 ‰, but only *C. danae* was captured there in July when salinity was about 38 ‰. Large male *C. sapidus* were captured in the headwaters of St. Joseph's Bay and in the Guadalupe River which drains into it, in July, August, and September. Salinity in the river at the time and place of capture was about 20 ‰.

2. *C. sapidus* were plentiful in the Laguna Madre in February, 1956, at a salinity of 38 ‰ and a temperature of 22°C.

3. They were also plentiful there in August at S = 58 ‰ and T = 33°C.

4. They were scarce there in December at S = 48–58 ‰ and T = 20°C, although crabs captured then were hypo-regulating.

5. Crabs from Austwell, acclimatized to normal sea water and subjected to hypersaline stress showed some regulatory ability and great salinity tolerance.

6. Crabs captured in the Laguna in December and treated as in "5" died rapidly, and did not regulate as well as crabs in "5."

While seasonal variations in distribution might well be due to factors other than decreased regulatory ability, points 3 and 5 indicate that high temperature does not impair ability to withstand high salinity.

Although *C. sapidus* from the Laguna differed in response to hypersaline stress from open bay and river crabs, the evidence for genotypic physiological differences is not extensive. Responses to osmotic stress varied, but representatives of the two populations always behaved as separate groups. It was shown by Odum (1953) that *C. sapidus* from Florida rivers could survive transfer from normal sea water to very dilute water if an intermediate salinity stage was used. This was found true for river crabs in Texas, but not for Laguna crabs, although periods of acclimation to normal sea water were not equal. In two out of three tests, Laguna crabs withstood high salinity better than river crabs after both groups had been acclimated to 100% S.W.

Comparison of *Uca* and *Ocypode* with *Callinectes* reveals both similarities and differences. Both groups can withstand salinities up to twice normal sea water, but the land crabs regulate blood concentrations of all ions and (probably as a consequence) osmotic concentration, within relatively narrow limits, while blue crabs tolerate a greater rise in total blood concentration and regulate mainly magnesium and sulphate. Abso-

lute concentrations of magnesium were lower in the blood of *Ocypode* than in *Callinectes*, while blood sulphate concentrations were just the opposite (*i.e.*, lower in *Callinectes*). Land crabs show a decrease in urinary sodium concentration, either in response to salinity or temperature stress; this response was not found in blue crabs. In both land crabs and blue crabs, the antennary gland appears to function in the regulation of magnesium and sulphate. Land crabs (except possibly *Pachygrapsus*) also seem to regulate potassium by way of the urine, while in *Callinectes* both blood and urine potassium are high. The higher total blood concentration of *Callinectes*, under hypersaline stress, compared to *Ocypode*, is probably due to difference in sodium and chloride regulation; both of these substances are well-regulated in *Ocypode*. Evidence implicating the gut in water absorption and salt excretion (in both types of crabs) is worthy of verification and further testing.

If the conclusions of Potts (1954) concerning the energetics of hyper-regulation can be reversed, the most efficient means of meeting hyper-osmotic stress would be to allow a slight rise in blood concentration. Both types of crabs use this mechanism to some extent, but it is most pronounced in *Callinectes*, where stress is continuous. Increased stress would require water conservation and salt excretion against a gradient. Production of a hypertonic urine would accomplish this, but evidence for its occurrence is not impressive. Prosser *et al.* (1955) did not find hypertonic urine in *Pachygrapsus*. In *Uca* and *Ocypode* slight urine hypertonicites were found, both in this investigation and in that of Green *et al.* (1959), but the cessation of urine production in air makes this observation of doubtful value. In blue crabs, during the first two days of high salinity stress, U/B and stomach fluid to blood ratios reached 1.2, but declined to under 1.05 by seven or eight days, as blood concentration rose. It may be that slight urine and stomach fluid hypertonicities, combined with a large flux of water through the animal, play some part in hypo-regulation. Another factor which may affect hypo-regulation in both land and blue crabs is the permeability of the body surface. Potts (1954) stressed its importance. An inverse relationship between permeability and regulatory ability in crabs has been reported by Gross (1957), who suggested that regulating mechanisms might be present in poor or non-regulators, but the mechanisms might be cancelled out by high permeabilities. Permeabilities of the body surface of *Callinectes* and *Ocypode* should be measured and compared.

Hypo-regulatory ability of land crabs decreases at high temperatures, while in blue crabs from the Laguna Madre it either increases or is insensitive to temperature. While several workers have reported changes in blood concentrations of euryhaline forms between winter and summer, actual tests of the effect of temperature on regulatory ability are not numerous. It was shown in the present investigation that *Uca pugnax* from Woods Hole regulated blood better (in 190% S.W.) at 21° than at 10 or 30°C. It would be interesting to compare northern and southern populations of *Uca* in this manner (using smaller temperature increments) to see if the temperatures of maximal regulation differed. The same thing should be done with *Callinectes*. Individuals of this species from the Laguna Madre differed from individuals from a neighboring brackish water population with regard to salinity-temperature tolerance, and may differ even more from northern populations. In any case, it is evident that salinity and temperature tolerance are interdependent, and cannot be considered separately.

Summary

1. Blood of urine concentrations of Na, K, Ca, Mg, Cl, and SO_4 are given for *Ocypode albicans* in external concentrations from 14 to 197% S.W. All ions are regulated to some extent in all salinities at temperatures between 12 and 25°C., but regulatory ability is reduced at temperatures of 29–35°C.
2. Temperature has a pronounced effect on hypo-regulatory ability of both *Ocypode* and *Uca*. Neither species can survive combined high temperature and high salinity; *Uca* regulates blood better (in 190% S.W.) at 21° than at 10 or 30°C.
3. Decreased urine Na concentrations occur in *Uca pugnax*, *Ocypode albicans*, and *Cardisoma guanhumi* when subjected to hyper-saline stress. In *Ocypode*, the effect is most pronounced at high temperature.
4. In *Uca* and *Ocypode*, injection of $MgCl_2$ alters urine Na concentration. The latter increases if initially low, decreases if initially high.
5. *Callinectes sapidus* has limited hypo-regulatory ability for total blood concentration and marked ability to regulate blood magnesium and sulphate, both in a high salinity lagoon and in the laboratory.
6. *C. sapidus* from the high salinity lagoon are more tolerant of high salinity and less tolerant of low salinity than are crabs from a brackish river, at least in summer, but evidence for a genotypic difference is not conclusive.
7. *C. sapidus* from the Laguna Madre seem to withstand combined high temperature and high salinity better than other crabs mentioned in the literature.
8. Some evidence implicating the gut in osmotic and ionic regulation (especially of magnesium and sulphate) is presented for both *C. sapidus* and *Ocypode albicans*.

Acknowledgments

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Osmotic and Ionic Concentrations in the Mantis Shrimp *Squilla empusa* Say[1]

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Abstract

Osmotic and ionic concentrations of body fluids and muscle in the stomatopod, *Squilla empusa*, were analyzed as a function of environmental salinity. Individuals survived gradual changes in salinity down to 13 ‰ as correlated with their distribution with six hours required for isosmotic equilibrium. Individuals survived rapid salinity changes between 22 to 47‰. With decreasing salinity below 21‰, specimens showed hyperosmotic regulation of serum with sodium, chloride and calcium tending to remain constant. In the muscle, sodium and chloride declined, potassium remained constant, and calcium and magnesium increased.

Large differences in composition of fluids were found in recently handled specimens.

In normal sea water serum cations and chloride accounted for 95% of the osmotic pressure, but with increased dilution they accounted for only 67% due to the increase of non-protein nitrogenous compounds.

Introduction

Osmotic and ionic regulation have been studied extensively in crustaceans. Several important works review this subject (Krogh, 1939; Prosser *et al.*, 1950; Beadle, 1957; Robertson, 1957, 1960; Schlieper, 1958; and Nicol, 1960).

Body fluids of most marine crustaceans are essentially isosmotic with the environment and show little regulation, although all show at least a limited degree of ionic regulation. Such poikilosmotic and usually stenohaline forms are represented by *Maja* (Duval, 1925), *Hyas* (Schlieper, 1929), *Portunus* (Margaria, 1931; Schwabe, 1933), *Lophopanopeus* and *Specocarcinus* (Jones, 1941), *Cancer antenarius* (Jones, 1941; Gross, 1957); *Cancer gracilis, Callianassa, Upogebia, Emerita,* and *Pugettia* (Gross, 1957).

Forms which show limited osmoregulation tend to invade brackish water. In brackish water their body fluids are slightly hyperosmotic, but when in sea water usually they maintain isosmoticity. Examples of this type of regulation are represented by *Cancer pagurus* (Schlieper, 1935), *C. magister, Hemigrapsus,* and *Rithropanopeus* (Jones, 1941) and *Asellus* (Lockwood, 1959). Similar regulation occurs in *Carcinus* (Duval 1925; Schlieper, 1929).

Hyposmotic regulation of body fluids when in sea water or concentrated salt water occur in *Ocypode, Cardisoma, Gecarcinus,* and *Grapsus* (Perse, 1932), *Pachygrapsus*

[1] Data on the effects of changing salinity on *Squilla empusa* are extracted from a Masters Thesis in Zoology (Marine Science) submitted by the first author to the Graduate Faculty of the University of Texas. Other data are the result of joint effort.

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(Schwabe, 1933b; Jones, 1941), *Leptograpsus* and *Heloecius* (Edmonds, 1935), *Leander* and *Palaemontes* (Panikkar, 1941), *Uca* (Jones, 1941) and *Artemia* (Croghan, 1958a). Body fluids of these crustaceans are hyposmotic in normal or concentrated sea water and usually hyperosmotic in brackish water.

Several papers deal with the effects of rapid and gradual changes in concentration of the medium on the osmotic and ionic concentrations of body fluids of crustaceans. In general, stenohaline forms do not regulate their blood osmotic concentration to either acute or slow changes (Schlieper, 1929; Duval, 1925; Gross, 1957). In contrast, euryhaline forms, including those of terrestrial habitat, have the ability to regulate concentration of their body fluids to sudden or slow changes of environmental salinity (Edmonds, 1935; Prosser, *et al.*, 1955; Gross, 1957; Green, *et al.*, 1959; *Croghan*, 1958a and b; Lockwood, 1959). For the euryhaline prawn, *Palaemonetes varians*, Panikkar (1941) found that they could survive in 15 per cent sea water when quickly transferred from normal sea water. Using slow dilution techniques he found *Palaemonetes* would survive in 0.3 per cent sea water.

Ionic regulation of several marine crustaceans in normal sea water has been studied by Robertson (1939, 1949 and 1953). He found that all ions in the blood varied from their concentrations in the medium. The largest ionic deviations from sea water, and particularly the lowest magnesium concentrations, were found in the more active crustaceans. Ionic regulation of marine crustacea in varying concentrations of the medium has been investigated by several workers. In the prawn, *Palaemon*, potassium, calcium, magnesium and sulphate are relatively constant but sodium and chloride decrease with environmental dilutions to 50 per cent sea water. At this dilution they are slightly higher than the environmental concentrations of sodium and chloride. Instances of active ionic accumulation have been demonstrated among the following species in dilute media: *Eriocheir* (Krogh, 1938; Koch, 1954; Koch, *et al.*, 1954), *Carcinus* (Webb, 1940), *Artemia* (Croghan, 1958 a and b) and *Asellus* (Lockwood, 1959).

Muscle ionic and osmotic regulation of marine crustacea have not been studied extensively. Shaw (1955 a and b, 1958 a and b) found that the muscle fibers of *Carcinus* are probably always in osmotic equilibrium with the blood. Apparently calcium and magnesium ions are passively distributed, whereas sodium ions are actively pumped from the cell and potassium ions are accumulated. Robertson (1957) indicates that cellular potassium does not stand in Donnan equilibrium with extracellular potassium in crustacea except for *Carcinus*.

In spite of the many studies that have been performed on aquatic crustacea, osmotic and ionic regulation in various sea water concentrations for the stomatopod mantis shrimps have not been investigated. Ionic regulation of *Squilla mantis* has been studied in normal sea water (Robertson, 1953). He found *Squilla* to have a similar type of ionic regulation as in several purely marine decapods, *i.e.*, accumulation of cations except for magnesium.

This investigation reports osmotic behavior of the mantis shrimp *Squilla empusa* and also ionic changes in body fluids and muscle as a function of salinity of the external medium. *Squilla empusa* commonly inhabits coastal seas and the bottoms of shallow muddy bays where the salinity is to a varying degree affected by fresh water drainage.

Materials and Methods

Collection and Care of Animals

Squilla empusa were collected from Corpus Christi Bay, Aransas Pass Channel and the Gulf of Mexico, Texas, with a 25 foot otter trawl. Twenty minute hauls were made each time. The collected animals if not immediately sampled were kept on board in running sea water until transferred to the laboratory. When not used experimentally, the animals were fed pieces of fresh fish or shrimp once a day. Food residues were removed as soon as possible to avoid contamination. Water in the holding tank was refilled daily with incoming tidal water from the Aransas Pass Channel. Salinity of this water fluctuated between 29 and 31 parts per thousand (‰). Special care was taken to refilter water in all experimental tanks.

Analytical Methods

Blood samples were collected with a glass cannula inserted into the ventral venous sinus. Blood was gently sucked from the sinus and discharged below the surface of ion-free paraffin oil in 15 ml centrifuge tubes. After collection, blood samples were placed on ice until analyses were started, usually within two hours. The blood samples were centrifuged and the clear blue serum pipetted off for chemical analyses.

Muscle samples, of approximately one gram wet weight for chloride determinations and 200 mg wet weight for flame analysis, were excised from the abdominal region of the dorsal muscle mass of each animal. After weighing, drying and reweighing, samples were mashed in a beaker and then digested in 0.2 ml of nitric acid and 2 ml of superoxol following the technique of Gordon (1959). The digested samples were filtered and diluted to 10 ml.

Serum freezing point depressions were determined with a Fiske Osmometer using 0.2 ml samples. Results are reported as milliosmols (mO) and/or as degrees centigrade depression.

The method of Schales and Schales (1941) was used for all chloride determinations. Water samples were titrated directly, but serum samples were digested with 0.2 ml of concentrated nitric acid and 2 ml of superoxol. The digested samples were diluted to 10 ml and centrifuged to remove fragments. A 2 ml portion of the diluted sample was used for titration.

Sodium and potassium were measured with a Beckman DU flame photometer by the direct method at 590 and 770 millimicrons. Calcium and magnesium were analyzed also with a direct method at 422.7 and 371 millimicrons, following the technique of Prosser, *et al.*, (1955). Due to interference efforts and low emission for these bivalent cations the error in their analysis might be appreciable.

Serum protein was estimated by the method of Robinson and Hogden (1941) using 3 ml samples of serum. Trimethylamine oxide content of serum was determined by the method of Dyer (1945) with 0.2 ml samples, while total non-protein nitrogen was obtained for 0.5 ml samples by standard micro-Kjeldahl technique.

Experimental Methods

Blood samples were collected immediately after recovery of mantis shrimp from the trawl. At the same time, the bottom water was collected for chemical analysis with a Kemmerer water sampler.

Several animals were transferred into a holding tank for two days before sampling to determine if any differences occurred in the body fluids due to handling and confinement.

In several experiments mantis shrimp were subjected to rapid salinity changes both above and below normal salinities (29–31 ‰). In these experiments distilled water was used to dilute sea water, while sea water was boiled to increase salinity. Changes in sea water concentration, whether diluted or concentrated, were made volumetrically. Specimens were transferred into several different concentrations and sampled at progressive intervals to determine how rapidly they adjusted the concentration of their body fluids.

In other experiments mantis shrimp were subjected to more gradual salinity changes. In these experiments the medium was diluted every 24 hours with water of salinity 2 ‰ from a natural pond. Body fluids from three specimens and muscle from one specimen were analyzed after 24 hours at each concentration.

Osmotic and Ionic Concentration of Serum and Ionic Concentration of Muscle of *Squilla empusa* at Environmental Salinities

Serum Osmotic Concentration

Osmotic concentrations of serum of *Squilla empusa*, as measured by freezing point depression, were found to be isosmotic or slightly hyperosmotic to the surrounding sea water (black circles, Fig. 1). However, serum was slightly hyposmotic with respect to the environment (triangles, Fig. 1) when specimens were held in the laboratory for one or two days. The data indicate that trawling induced a slight hyperosmoticity in the

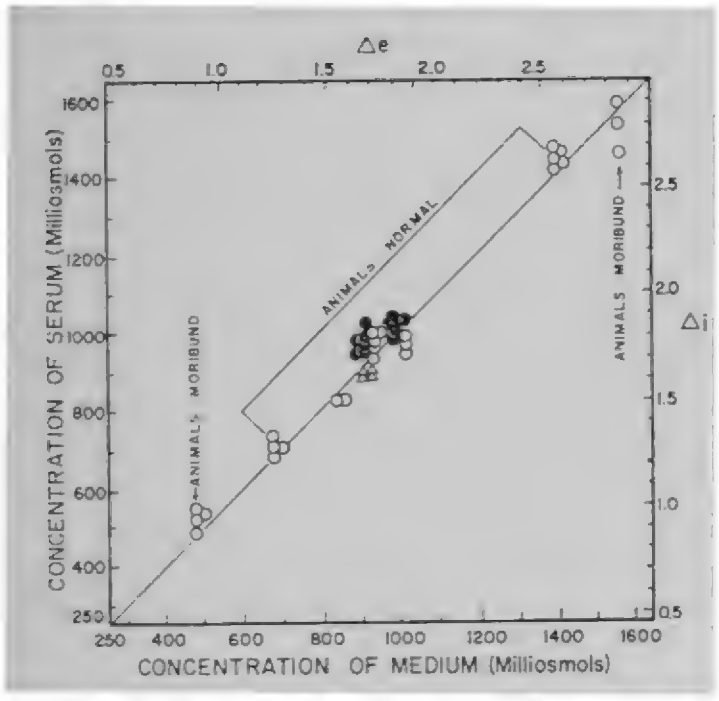

FIG. 1. Relationship of body fluid osmotic concentration to environmental osmotic concentration in *Squilla empusa*.

Black circles represent data for specimens sampled immediately after capture; triangles data for specimens held for 48 hours in the laboratory; and open faced circles result for specimens subjected to rapid changes in salinity. One osmol is equivalent to one mole glucose per kilogram of water or —1.86° C freezing point.

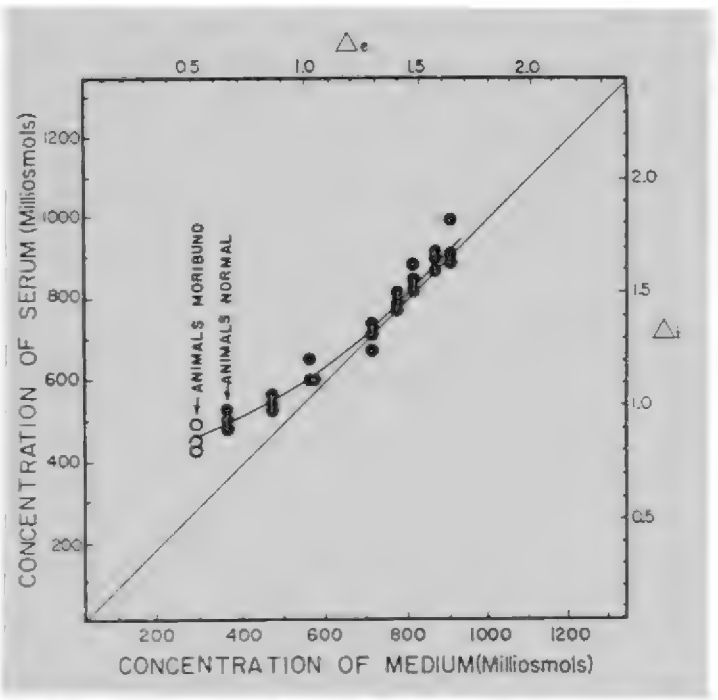

FIG. 2. Relationship of body fluid osmotic concentration to environmental osmotic concentrations for *Squilla empusa* when subjected to slow dilution.

Each group of data represents the osmotic concentration of fluids after 24 hours exposure to the respective salinity. All specimens were subjected to progressive dilution every 24 hours.

body fluids. Statistical comparison reveals that the mean milliosmolal concentration for each group is significantly different [P ($|t| > 3.355$) = 0.005, where t = 14.05].

Similar results have been obtained for isosmotic vertebrates after handling (McFarland and Munz, 1958). However, attempts to induce hyperosmoticity through artificial handling of mantis shrimp, previously held in the laboratory, produced variable results. Some specimens were hyperosmotic, whereas others were isosmotic or hyposmotic.

Serum Ionic Concentration

The concentration of sodium, potassium, calcium, magnesium and chloride in the serum of *S. empusa* immediately after capture and after being held for two days in the laboratory are shown in Table 1. Serum magnesium and chloride were at lower concentration than environmental concentrations whether sampled immediately after collection or after holding, whereas sodium was lower in concentration only from specimens held in the laboratory. Potassium approached twice the environmental concentration regardless of sampling conditions, whereas calcium was the same in immediately sampled specimens. In the specimens held for 48 hours calcium was 1.45 times as concentrated as in sea water.

Table 1

Concentration of ions in blood serum of *Squilla empusa* from trawl collections and after holding in the laboratory for 48 hours*

Sample	Milliosmols	Ion concentration expressed as mEq/liter					
		Na^+	K^+	Ca^{++}	Mg^{++}	Cl^-	Sum of ions
Trawl Collection, sampled immediately							
Serum	1003.6	441.8	15.0	19.2	42.0	430.9	948.9
Sea water	987.0	394.0	9.4	20.0	81.0	502.0	1006.4
Cation to chloride ratio of water	.....	0.784	0.018	0.040	0.161	1.000	.....
Holding Experiment, adapted							
Serum	897.7	348.0	17.0	33.6	52.6	401.7	852.9
Sea water	924.6	367.5	10.5	23.0	80.0	451.7	932.7
Cation to chloride ratio of water	.....	0.814	0.023	0.051	0.177	1.000	.....
Oceanic Water†							
Cation to chloride ratio	.....	0.859	0.018	0.037	0.195	1.000	.....

* Errors of analysis for sodium and potassium were less than ±3%; chloride error was +5.5% and can account for the constant low cation to chloride ratio of trawl collection sea water compared to holding experiment sea water; mean error for calcium was +5% while for magnesium it was ±2.2%. Emission error for the latter two elements can be high and absolute error thus might be considerable.

† Sverdrup et al., 1942.

The sodium, potassium, magnesium, calcium and chloride in the serum, for the specimens held for 48 hours before sampling, account for slightly more than 95 per cent of the total osmotic pressure of the body fluids. Since some calcium is most probably in bound form as a calcium-protein complex, the actual total osmotic effect of the ions is certainly somewhat lower than 95 per cent. Presumably the difference is made up by anions, such as sulfate, and by nitrogenous compounds. Unfortunately, no data are available on the concentration of sulfate while our data on nitrogenous constituents are not sufficient to generalize. As in other crustaceans, sodium and chloride are the most important osmotic constituents, making up 83.5 per cent of the total serum osmotic pressure ($749.7 / 897.7 \times 100$).

Examination of the ratio for the various cations to the concentration of chloride for

the environmental waters from which the mantis shrimp were obtained and for oceanic water indicates that potassium is normal, sodium and magnesium are low, and calcium is slightly high. The effect of such changes in the ionic constituents of the sea water on ionic balance of *S. empusa* are difficult to equate. However, in Table 2 the relative ionic levels as a per cent of total cation concentration are compared with several other crustaceans. Examination of the data for *S. empusa* when hyperosmotic to the environment (sampled immediately) and when slightly hyposmotic to the environment (sampled after 48 hours), again indicates that handling seriously affects the ionic concentrations of the serum, as well as the total osmotic pressure. All ions are affected but sodium, chloride and calcium are most affected on an absolute basis, while magnesium and potassium are changed to a lesser degree.

Comparison of data for both hyperosmotic and hyposmotic specimens of *S. empusa* with other crustaceans reveals that ionically, *S. empusa* is more like crustaceans that show poor osmotic regulation such as *Maja squinado* and *Hyas araneus* (Bethe and Berger, 1931) than crustaceans showing fair to excellent regulation (Table 2). Careful examination of values in this table indicates that the various crustacean species can be classed as forms with ratios either closer to the hyperosmotic specimens of *S. empusa* or to the hyposmotic specimens. For instance, the values for *Maja squinado* are more like

TABLE 2

Relative ionic concentration of serum in *Squilla empusa* compared to other crustacea. Numbers in brackets are ratios for sea water.

Species	Total cations (mEq/liter)	Ratio to total cations (based on mEq/liter) Na^+	K^+	Ca^{++}	Mg^{++}	Cl^-
STOMATOPODA						
Squilla empusa						
Hyperosmotic specimens	518.0	0.853(0.781)	0.029(0.019)	0.037(0.040)	0.081(0.161)	0.832(0.990)
Hyposmotic specimens	451.2	0.771(0.764)	0.038(0.022)	0.074(0.048)	0.116(0.166)	0.890(0.950)
BRACHYURA						
Stenohaline						
*Maja squinado**	764.1	0.770(0.917)	0.045(0.020)	0.071(0.010)	0.115(0.053)	0.812(0.943)
*Hyas araneus**	620.2	0.820(0.790)	0.020(0.018)	0.038(0.034)	0.120(0.156)	0.836(0.898)
*Cancer pagurus**	638.4	0.847(0.790)	0.028(0.018)	0.038(0.034)	0.085(0.156)	0.810(0.898)
Cancer pagurus†	596.7	0.842(0.771)	0.020(0.016)	0.046(0.034)	0.092(0.179)	0.864(0.864)
Euryhaline						
*Carcinus maenas**	662.4	0.871(0.790)	0.019(0.018)	0.039(0.034)	0.080(0.156)	0.820(0.888)
Pachygrapsus crassipes§	517.0	0.891	0.018	0.052	0.039	....
Homarus americanus¶	516.6	0.881	0.018	0.066	0.035	0.915 .....
Homarus gammarus†	576.0	0.898(0.771)	0.025(0.016)	0.052(0.034)	0.025(0.179)	0.924(0.864)
Nephrops norvegicus‡,**	570.8	0.906(0.771)	0.013(0.016)	0.049(0.034)	0.032(0.179)	0.908(0.864)
Palinurus elephas‖	615.4	0.884	0.017	0.044	0.055	0.905 .....

* Bethe and Berger, 1931.
† Robertson, 1939.
‡ Robertson, 1949.
§ Schlatter, 1941.
¶ Cole, 1940.
‖ Hemingsen, 1942.
** Sea water ratios for *Nephrops* determined by Robertson (1939).

the values for hyposmotic *S. empusa*, whereas values for *Cancer pagurus* are much more like hyperosmotic *S. empusa*. The ionic and freezing point data indicate that results depend to a large degree on the previous history of specimens. The inability to consistently induce artificial hyperosmoticity in *Squilla* makes interpretation difficult, since the precise osmotic and ionic status of individuals under natural conditions cannot be ascertained from the data. Normal osmotic and ionic concentrations in crustacea need careful investigation.

In spite of this uncertainty, it can be said that *S. empusa* is relatively a poor regulator. Unlike *Squilla mantis* (Robertson, 1949) it shows relatively high values for magnesium. Since *S. empusa* is relatively active these results are in contrast with Robertson's correlation that reduction in magnesium in marine invertebrates goes hand in hand with rapid movement. However, until replicate analyses of magnesium are made by chemical techniques other than flame photometry, which is subject to interference emissions, the high values reported here must remain quite doubtful.

Robertson (1949, 1953) compares the $Na + K/Ca + Mg$ ratio for several marine invertebrates. He finds values below 4.2 for relatively inactive crustaceans and for other types of invertebrates whether active or inactive. Values from 6.7 to 11.5 were found for active crustaceans, like *Pachygrapsus* and *S. mantis*. Values of this ratio for *S. empusa* were 4.2 for hyposmotic specimens and 7.46 for hyperosmotic forms. These differences are primarily the result of large increases in sodium and losses in calcium for the hyperosmotic forms.

Muscle Ionic Concentration

Analysis of the major cations and chloride ion in muscle of *S. empusa*, sampled immediately after capture and after laboratory adaption for 48 hours, indicate that large changes in the concentration of ionic species occur (Table 3). Sodium, calcium, magnesium, and chloride are all less concentrated in adapted animals (hyposmotic serum) than in specimens that are not given time to adapt (hyperosmotic serum). Only potassium is unaffected. Comparison of individual ion concentrations of muscle tissue for non-adapted specimens to adapted specimens suggests that when animals are roughly handled sodium, calcium, magnesium and chloride rapidly invade the extracellular muscle-tissue spaces. The ratios of values sampled immediately to values obtained after

Table 3

Relative ionic concentration of muscle in *Squilla empusa* compared to other crustacea

Species	Concentration of ion in mEq/kg water, Mean SE (number samples)				
	Na^+	K^+	Ca^{++}	Mg^{++}	Cl^-
Squilla empusa					
Sampled immediately*	163.5±12.8(7)	87.4±7.0(7)	16.9±3.1(7)	42.5±3.0(7)	176.7±13.5(7)
Sampled after adaptation†	87.4±18.9(4)	89.9±6.0(4)	7.1±1.3(4)	29.6±4.1(4)	109.3± 6.3(4)
Nephrops norvegicus‡	83.2	166.6	10.4	38.2	109.9
Carcinus maenas§	54.0	146.0	10.0	34.0	53.0

* Sampled after capture, 33‰ sea water.

† Adapted 48 hours in laboratory at 32‰ sea water.

‡ Robertson, 1957.

§ Shaw, 1958b.

48 hours in Table 3 are: Na = 1.87; K = 0.975; Ca = 2.38; Mg = 1.44; and Cl = 1.62. Only the ratio for potassium remains close to unity while the ratios for sodium, magnesium and chloride are high but similar.

With the exception of potassium the concentration of muscle tissue ions for the specimens held for 48 hours agrees favorably with the few published results for other crustaceans (Table 3). Characteristically, potassium is concentrated in the muscle tissue and is approximately 5.5 times higher than in serum. The apparent stability of potassium in the muscle tissue between roughly handled and adapted animals does not negate its possible movement into the extracellular spaces. Movement of potassium into the extracellular muscle-tissue spaces could remain undetected due to the large amounts of the ion present in the tissue as compared to the serum.

Osmotic Changes in *Squilla empusa* When Exposed to Different Concentrations of Sea Water

Effect of Rapid Immersion in Dilute Sea Water

Specimens previously held for 48 hours in sea water with an osmotic concentration of 907 mO were abruptly transferred in groups of 10 to tanks containing varous dilutions of sea water. Considering the water with a concentration of 907 mO as 100% sea water, the concentrations of various tanks were: 92.5% (837 mO); 75% (682 mO); 52.5% (476 mO); 27% (246 mO); and 12.5% (112 mO). Water temperature during the 24 hour period of experimentation varied from 18.0° to 20.5°C.

Behavioral responses of the specimens when placed directly into the various salinities were as follows:

100% sea water. Specimens were normal throughout the experimental period showing no signs of stress or unusual activity, such as loss of equilibrium.

95% sea water. No differences were noted from animals in 100% sea water.

75% sea water. Immediately after introduction a marked reduction in motility was noted, but equilibrium was not lost. Several of the specimens attempted to propel themselves from the water. After one hour, however, normal movements were observed. Further behavioral deviations were not observed for the remaining 23 hours of the experiment.

52.5% sea water. Five of the ten specimens in this group immediately sank upside down to the bottom and lay motionless except for slow movements of the swimmerets. The other specimens did not show upsets in equilibrium but were much less active than controls. One hour after introduction one specimen was dead, while by six hours six animals were sampled and the remaining four shrimp were dead.

27% sea water. All specimens responded by turning upside down on the bottom. All were moribund, only the swimmerets showing motion. After one hour all animals but one were dead.

12.5% sea water. All animals responded as in 27% sea water. After 30 minutes nine were dead and at 50 minutes the remaining shrimp ceased all movements.

Dilutions of sea water greater than 75% are rapidly lethal to *S. empusa* under conditions of immediate transfer from normal sea water. Osmotic concentrations of serum removed from specimens at progressive times during the experiment for 100, 92.5, 75

and 52.5% sea water reveal that serum becomes isosmotic to diluted sea water after approximately six hours exposure.

Effect of Rapid Immersion in Concentrated Sea Water

A separate but otherwise similar experiment to the acute dilution experiment was performed for concentrations of sea water greater than 100%. As in the dilute experiments isosmotic adjustment of the body fluids occurred within six hours. Behavioral reponses of these groups to increased salinity were:

100% sea water. As before, this group served as a control and showed normal movements and equilibrium throughout the experiment which was extended to 60 hours.

109% sea water. This group showed no noticeable changes in behavior.

149% sea water. No noticeable change was observed in the behavior of this group throughout the entire 60 hours except that one animal died after seven hours exposure.

168% sea water. After 30 minutes exposure two specimens were upside down and immobile. The remainder showed a reduction in motility. At one hour all specimens were upside down and showed only slight movements of the swimmerets. At six hours all specimens were moribund. This group was discontinued after six hours exposure.

200% sea water. Immediately after immersion all animals in this group lost equilibrium, lay upside down on the tank bottom, and showed only slow movements of the swimmerets. After one hour all motion ceased and the group was removed.

The results of dilution and concentration experiments show that *S. empusa* has no ability to osmoregulate its body fluids rapidly. Under acute conditions when previously adapted to salinities of approximately 31 ‰ (907 to 934 mO), the maximum salinity tolerance range varied from 22 ‰ to 46.5 ‰. Within this salinity range, *S. empusa* shows less behavioral deviations in response to increased salinity than to decreased salinity.

Effect of Slow Changes in Salinity

To test the possibility that *S. empusa* might survive at concentrations below 22 ‰, a series of groups, each containing three individuals, were placed in lower and lower salinities each day. Samples of serum were analyzed for one group at each salinity after 24 hours exposure. In contrast to results for rapid dilution (Fig. 1), isosmoticity of the serum at all concentrations does not occur (Fig. 2). Rather, at 78% sea water (considering the highest concentration for this experiment of 909 mO as 100% sea water) the serum of *S. empusa* becomes slightly hyperosmotic to the environment and at 39% sea water (335 mO) is about 41% more concentrated. At lower concentrations, the animals deviate from normal behavior and become moribund (Fig. 2).

These results indicate that *S. empusa* is osmotically a typical stenohaline crustacean and shows, at best, only a slight degree of osmotic regulation. It compares closely with *Cancer pagurus* (Duval, 1925).

Ionic Changes in Body Fluids Following Changes in Concentration of the Medium

Sodium, potassium, calcium, magnesium and chloride concentrations in serum, decrease with environmental concentrations. In Figures 3, 4, 5, 6 and 7 are plotted the

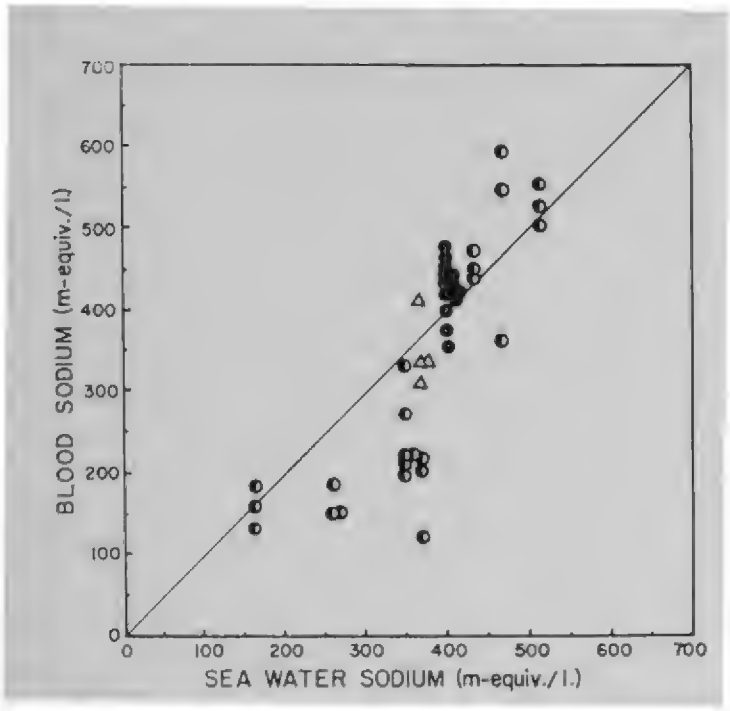

FIG. 3. Relation between serum sodium concentration and sea water sodium concentration.

Black circles are data for specimens sampled immediately after capture; triangles data for specimens held for 48 hours in the laboratory; and semi-open faced circles values for specimens subjected to slow dilution. The diagonal line through the origin represents equal concentration in serum and medium.

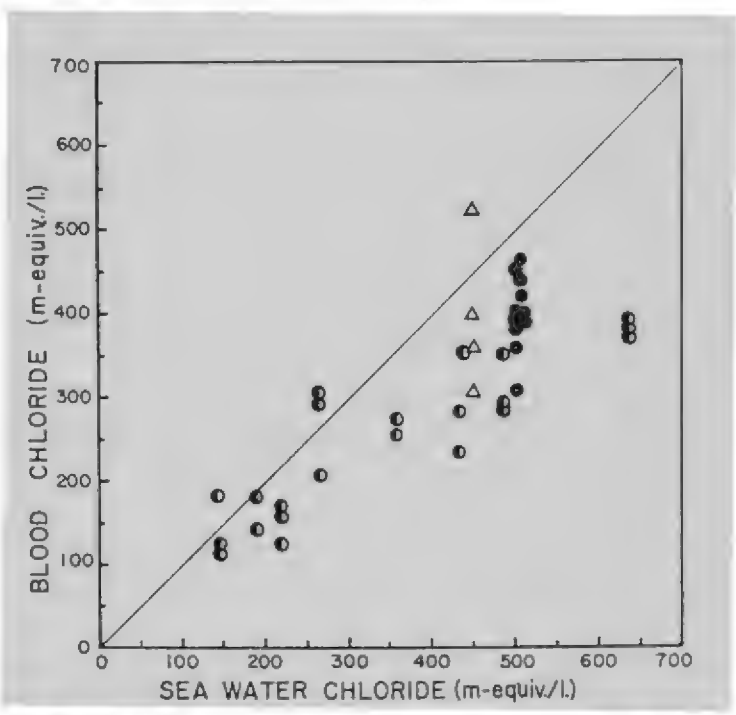

FIG. 4. Relation between serum chloride concentration and the sea water chloride concentration.

Symbols are the same as in Figure 3. The diagonal line through the origin represents equal concentration in serum and medium.

various data for *S. empusa* from the natural environment, holding experiments, and from slow dilution experiments. Values for rapid dilution experiments are not plotted since variation is large, although the same tendency for a decrease in concentration with dilution is evident.

A tendency for constancy in the concentrations of sodium (Figure 3), chloride (Figure 4), and to a larger extent calcium (Figure 6) are evident. This also is possible for magnesium (Figure 7). This constancy occurs in all four instances below 20 ‰ and is

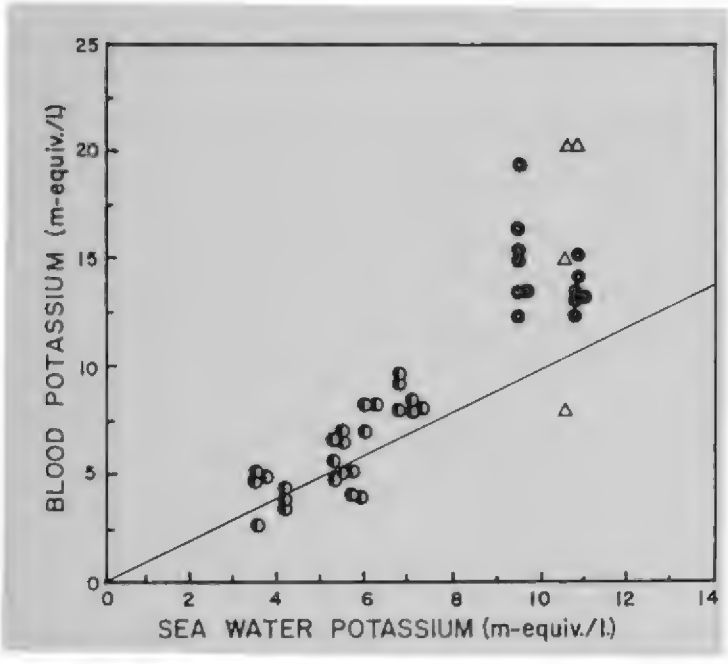

FIG. 5. Relation between serum potassium concentration and sea water potassium concentration.

Symbols are the same as in Figure 3. The straight line through the origin indicates equal concentration in serum and medium.

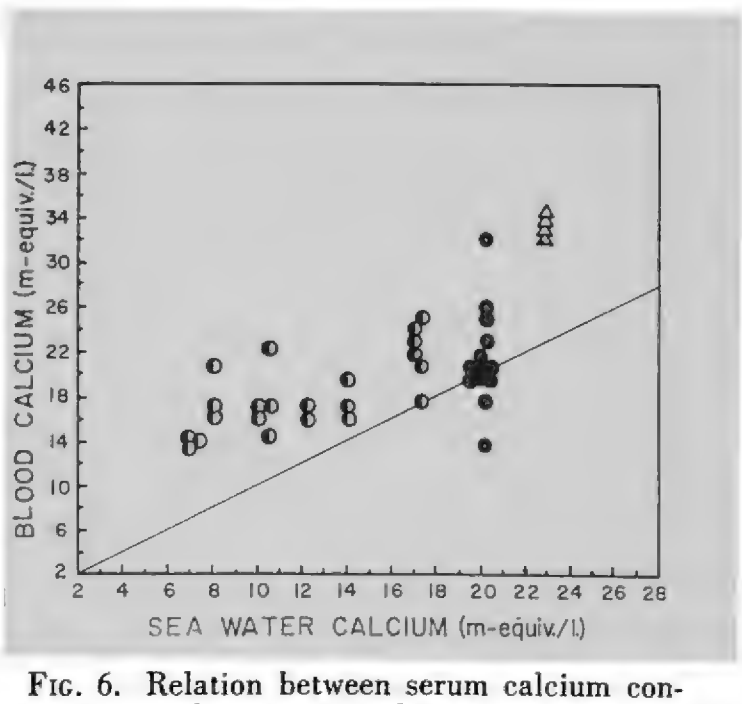

FIG. 6. Relation between serum calcium concentration and sea water calcium concentration.

Symbols are the same as in Figure 3. The straight line shows equal concentration in serum and sea water.

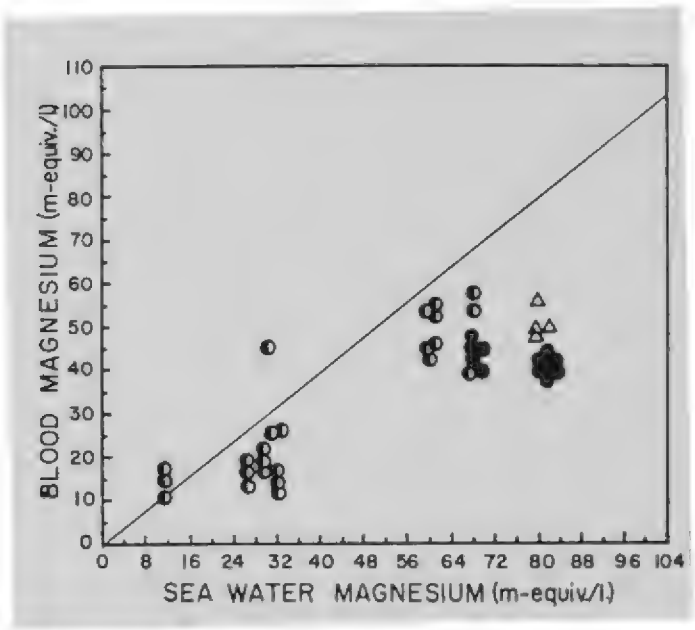

FIG. 7. Relation between serum magnesium concentration and sea water magnesium concentration.

The symbols are the same as in Figure 3. The straight line through the origin shows equal concentration in serum and medium.

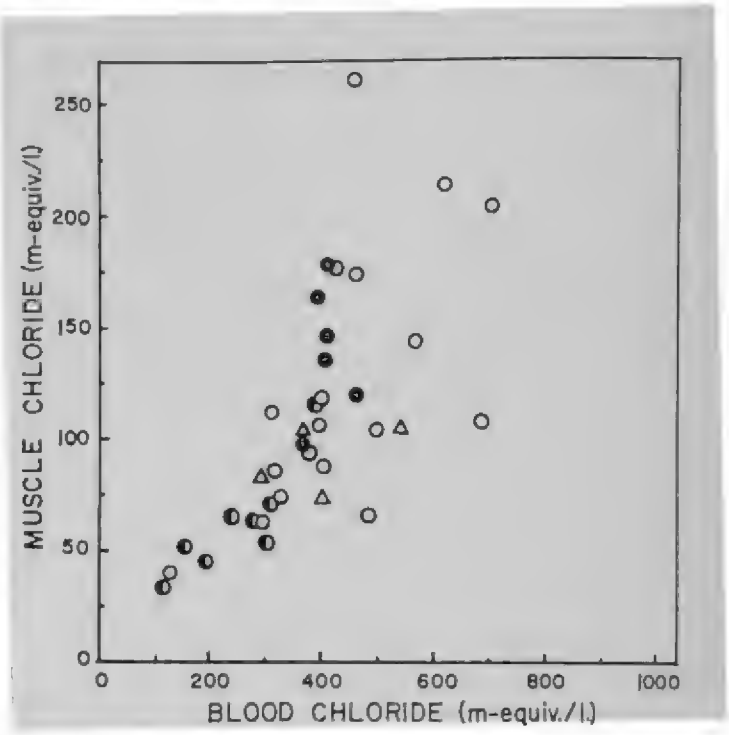

FIG. 8. Relation between muscle chloride concentration and serum chloride concentration.

Black circles represent data for specimens sampled immediately after capture; triangles data for specimens held for 48 hours in the laboratory; open faced circles result from specimens subjected to quick dilution in salinity; and semi-open faced circles values for specimens subjected to slow dilution in salinity.

correlated with the hyperosmoticity found in body fluids in the slow dilution experiments at environmental concentrations below 600 mO (Figure 2).

The osmotic effects of the various ions at different concentrations of sea water are indicated in Table 4. Interestingly, the relative concentrations of total cations and chloride, and of sodium and chloride to total serum osmotic pressure become less with decreasing environmental salinity. Below 60% sea water ionic contribution is essentially constant at 66–69% of the serum concentration. This is in contrast to the values of 95% found for animals held and handled carefully for several days before sampling. The differences certainly must be caused in part by unmeasured anions and by nitrogenous compounds.

In a separate experiment, *S. empusa* were subjected to slow dilution over a period of one week until the final sea water concentration was 50% of the initial concentration. In addition to freezing point and ionic analysis, the protein, non-protein nitrogen, and trimethylamine oxide concentrations of serum were determined (Table 5). The final

TABLE 4

Per cent contribution of cations and chloride to serum osmotic pressure. Specimens were held for 24 hours at each concentration and sampled.

Per cent sea water	Osmotic concentration of serum (m0)	Per cent total cations and chloride	Per cent sodium and chloride
100	931	104.0	95.0
95	900	102.0	93.3
89	857	93.8	86.0
85	786	77.8	68.8
78	701	77.0	71.5
60	620	66.5	60.0
51	528	69.5	63.0
39	502	67.4	60.0

TABLE 5

Distribution of serum constituents of *Squilla empusa* subjected to slow dilution of environmental salinity. Initial concentration of sea water was 32‰ (930 mO). Final concentration of sea water was 50 per cent. All values but K^+ and Trimethylamine (TMAO) are rounded to the nearest whole number.

Sample no.	Total conc. mO	mEq/liter					Per cent total cations and Cl^-	Protein g/liter	TMAO mg/liter	NPN mg/100 ml
		Na^+	K^+	Ca^{++}	Mg^{++}	Cl^-				
1	545	202	5.6	14	22	209	83	25	0.75	50
2	570	225	5.6	14	26	202	83	23	0.74	36
3	523	187	6.6	15	22	202	83	20	1.55	43
Mean	546	207	5.9	14	23	204	83	23	1.01	43
Sea water	463	180	4.9	8	39	255	94	....	.....	....

serum osmotic pressure was similar to previous experiments, but contributions of cations and chloride were higher (83% as opposed to 70%). Concentrations of protein in serum were quite low and only one-third of the value of 65 g/liter of plasma reported by Robertson (1960) for *Squilla mantis*. Trimethylamine oxide was exceedingly low and therefore contributed little if any osmotic effect.

In contrast, the non-protein nitrogen fraction was very high and exceeded every value reported by Florkin (1960) for a variety of crustaceans. However, even if these high concentrations of nitrogen were present as amino acids like alanine, glycine or glutamic acid they would not account for the osmotic difference of 92 mO between total concentration of serum and ionic species (546 minus 454, Table 5). Whether these ionic contributions to total serum osmotic pressure would have returned to normal (near 95%) for test periods in excess of 24 hours is unknown. The values of 104 and 102% reported for 100 and 95% sea water (Table 4) possibly are high because of the inclusion of protein-bound calcium in values for summed cations.

Ionic Changes in Muscle Tissue Following Changes in Concentration of the Medium

Concentration of sodium, potassium, calcium, magnesium and chloride were determined for muscle tissues of *S. empusa* both under natural conditions and experimental conditions. Data found for muscle ions in normal sea water concentrations were reported and compared with other crustaceans in Table 3.

Muscle concentrations of chloride and potassium ions in mEq/l are plotted against their respective serum concentrations in Fig. 8 (chloride) and 9 (potassium). Multiplication of individual muscle concentrations by 1.21 expresses the concentration in mEq/kg water (factor based on overall average water content of muscle).

A definite relationship exists between muscle and serum ionic concentrations for sodium and chloride ions. Both the sodium and chloride in muscle decrease with serum concentration. This tendency is less, however, where the animals have been subjected to sudden changes in salinity. Since both serum sodium and chloride tend to decrease with decreases in environmental concentrations (Fig. 3 and 4) the declines in muscle sodium and chloride indirectly reflect environmental changes in these ions.

The high correlation between muscle sodium and chloride (Fig. 10) indicates that they move jointly into and out of muscle tissue. Where deviations do occur they are

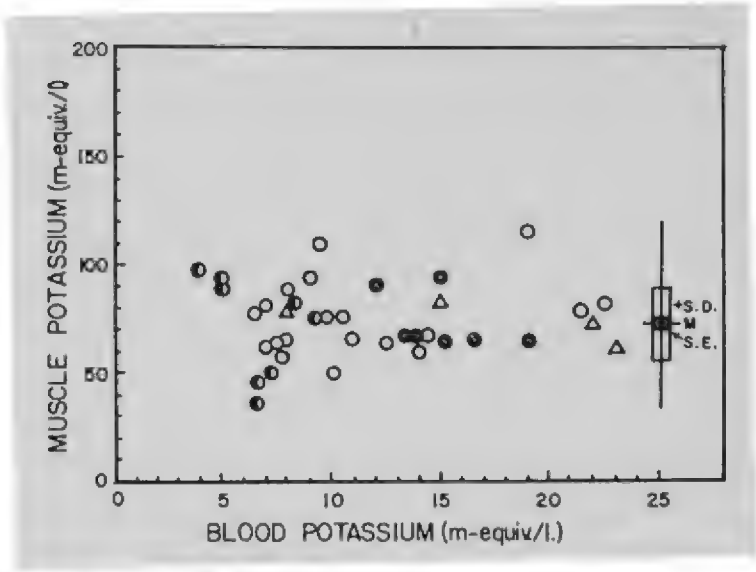

FIG. 9. Relation between muscle potassium concentration and serum potassium concentration. Symbols are the same as in Figure 8.

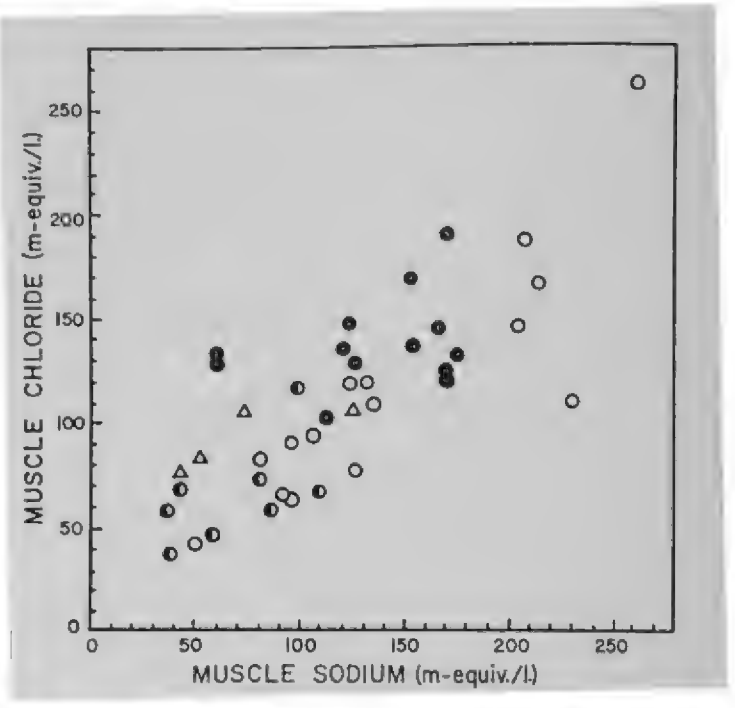

FIG. 10. Relation between muscle chloride concentration and muscle sodium concentration. Symbols are the same as in Figure 8.

correlated with acute changes in salinity, rather than with slow changes. These results are in keeping with the concept that muscle chloride and sodium are found primarily in the extracellular muscle spaces (Hayes and Pelluet, 1947; Steinbach, 1940; Conway, 1954; Gordon, 1959).

Muscle potassium, in contrast to sodium and chloride, remains relatively constant regardless of the serum potassium concentration (Fig. 9). Since serum potassium also declines with environmental potassium (Fig. 5), the constancy of muscle potassium supports the concept that it is primarily intracellular (Hayes and Pelluet, 1947; Gross, 1958). Shaw (1955b), in contrast to the constancy of muscle potassium found here for *Squilla empusa*, reports that in *Carcinus maenas* muscle potassium decreases from 150 mM/kg muscle water to 80 mM/kg muscle water as blood potassium declines from about 14 mM/liter to 8mM/liter. Below serum levels of 8mM/liter, muscle potassium was constant at 80 mM/kg muscle water. It is quite possible that muscle potassium values for *S. empusa* would change given more than 24 hours to regulate. However, exposure of animals to slow changes of external salinities for periods up to 11 days did not effect changes in muscle potassium concentration.

Concentrations of muscle calcium and magnesium as a function of serum calcium and magnesium indicate no apparent correlation. However, if the values for rapid dilution experiments, which show high variation, are ignored, a tendency can be detected for both muscle calcium and magnesium to increase slightly as an inverse function of their serum concentration. Changes are sufficiently slight, particularly for magnesium, to conclude that these concentrations are essentially constant in muscle as a function of changing serum concentration. In his work on *Carcinus*, Shaw (1955b), found that muscle calcium and magnesium were little affected by dilution of the environment.

Discussion

The inability of *Squilla empusa* to regulate body fluids homoiosmotically indicates that this species has long been primarily a marine crustacean. Species that show either fresh water or brackish water tendencies usually are hyperosmotic under such conditions and

show isosmoticity only to increased salinity, while euryhaline and terrestrial species show homoiosmotic regulation in either dilute or concentrated media (Robertson, 1960). Apparently the long residence of *S. empusa* as a marine crustacean has not necessitated the evolution of more efficient regulatory devices. Its intrusions into brackish waters are only marginal. Although as yet untested, it is probable that *S. empusa* achieves the degree of ionic regulation it exhibits much like other poikilosmotic crustaceans, namely, by selective secretion of magnesium and possibly sulfate in a urine isosmotic to the blood and environment. Whether this actually occurs must await analysis of the antennal gland excretions.

Abundant populations of *S. empusa* are found along the south Texas coast only in waters near or above 30 ‰ (Gunter, 1950). Of 92 animals collected by Gunter, during systematic trawl hauls, only six occurred below 30 ‰. Three were captured at 16.5 ‰, the lowest salinity at which they were encountered. In the Mississippi Delta, Parker (1956) captured *S. empusa* in relative abundance at salinities down to 25 ‰. Our collections in south Texas support these findings. *Squilla empusa* were encountered primarily in the open Gulf of Mexico or in the mouths of primary bays in spring and summer where salinity, when the mantis shrimp were abundant, seldom was less than 25–28 ‰.

The salinities observed with *S. empusa* in the field agree fairly well with the lower limit of 22 ‰ established by rapid dilution methods. In contrast, the lower limit of 12–13 ‰, established by slow dilution experiments, agrees with the experience of Mr. Anthony Inglis of the U.S. Fish and Wildlife Service. He reports that *S. empusa* is taken by bait fishermen from Galveston Bay, Texas, at salinities from 11 to 15 ‰.

Robertson (1957) indicates that of three crustaceans studied (*Eriocheir*, *Carcinus* and *Nephrops*) only in *Carcinus* did the ratios for potassium and chloride between muscle and serum show their concentrations to be the result of a Donnan equilibrium (Table 6). In this study, ratios of potassium in muscle to potassium in serum approximate ratios of chloride in serum to chloride in muscle, a condition that may indicate a Donnan equilibrium. Values of 3.96 for potassium and 4.32 for chloride were obtained (Table 6). However, values for slow dilution experiments give increasingly high potassium ratios, but constant chloride ratios. For instance at 100% sea water the ratios are 8.46 for potassium and 3.29 for chloride, whereas at 39% sea water they are 18.6 and 3.97, respectively. Such widely differing values are difficult to interpret, but *S. empusa* under normal environmental circumstances could be considered as having muscle ions, like potassium in Donnan equilibrium.

TABLE 6

Relative ratios of concentrations of postassium and chloride in muscle to those of blood serum

Species	$\frac{K_i}{K_o}$	$\frac{Cl_o}{Cl_i}$	Reference
Squilla empusa			
Hyperosmotic*	4.8	3.0	.....
Hyposmotic†	3.96	4.32	.....
Eriocheir sinensis	18.4	3.21	Robertson, 1957
Carcinus maenas	8.8	10.5	Robertson, 1957
Nephrops norvegicus	20.6	9.39	Robertson, 1957

* Values from animals sampled in the natural environment.
† Values from animals held in the laboratory for 48 hours.

Summary

(1) Osmotic and ionic concentrations of body fluids and ion concentrations of muscle for the stomatopod, *Squilla empusa*, are reported as a function of environmental concentrations.

(2) Freezing point depression of body fluids reveals that *S. empusa* is poikilosmotic above 23 ‰ salinity. When subjected to rapid changes in salinity of the environment it survives between 22 to 46.5 ‰, but initially shows upsets in equilibrium and behavior. At salinities beyond this range behavioral deviations are not overcome and the animals die. Regardless of the magnitude of salinity stress, about six hours are required for specimens to reach isosmotic equilibrium. When subjected to slow dilution the lower salinity tolerance of *S. empusa* is extended to 12–13 ‰. At approximately 21–23 ‰ specimens begin to show hyperosmotic regulation of serum. However, all specimens react slowly below 20 ‰.

(3) Analysis of serum ions indicates that sodium, potassium, calcium, magnesium and chloride all tend to decrease in concentration with dilution of the environment. Below 60% sea water sodium and chloride, and to a greater extent calcium, tend to remain constant. This correlates with the noted hyperosmoticity of the serum below 20 ‰.

(4) Sodium and chloride concentrations of muscle both decline with decreases in environmental and serum concentrations. In contrast, potassium remains constant, whereas calcium and magnesium show a slight tendency to increase.

(5) Comparison of analysis of body fluids of *S. empusa* immediately after collection and after holding for several days shows that considerable differences exist in concentration of ions and osmotic pressure. Animals that are not handled carefully are hyperosmotic to sea water and the concentrations of serum sodium, calcium, and chloride are all drastically changed. Such differences are sufficient to effect a complete displacement in the relative concentration of serum ions. Because of this, ionic balance in *Squilla* can appear more like that of active homoiosmotic crustaceans than like that of poikilosmotic crustaceans. It is concluded that extreme care must be taken in interpretation of reported results unless precise knowledge of how animals were handled is known.

(6) The serum cations and chloride account for 95% of the total osmotic pressure for *S. empusa* at normal sea water concentrations. With increased dilution of the environment they account for much less being only 67% of the total in sea water of 12–13 ‰. It is shown that the balance is made up in part by non-protein nitrogenous compounds, most probably amino acids, but not by trimethylamine oxide or high serum protein concentrations.

Acknowledgments

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Phosphorus Content of Some Fishes and Shrimp in the Gulf of Mexico

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Abstract

The total phosphorus composition was determined for ten species of fish and one species of shrimp found in the coastal and bay waters of Galveston, Texas. The results of the analyses, which were based on the entire animal, were compared with the few similar analyses that have been made on other marine species. Shrimp contained about 1.46% P of dry weight (0.35% of wet weight). Fishes contained 2.43 to 3.81% P of dry weight (0.47 to 0.84% of wet weight). A brief discussion of the biogeochemical phosphorus cycle is included.

Phosphorus is one of the most measured ingredients of sea water. This element in its ionic form as phosphate is vital to the production of plant life, and most marine scientists, therefore, consider it significant as an indicator of productivity. Phosphorus also occurs in particulate and dissolved organic compounds and in organisms. The importance of this element in food has resulted in chemical investigation of marine products. W. O. Atwater (1892) determined the phosphorus composition of many food fish and invertebrates; later data were summarized by Vinogradov (1953). Most of the work was based on specific organs, tissues, or parts, rather than the whole animal. This paper presents the phosphorus content of various fishes and shrimp based on the entire animal. The specimens analyzed included inhabitants of the coastal and bay waters of Galveston, Texas, and an undetermined species of lantern fish (family Myctophidae) taken about 50 miles southwest of the Mississippi Delta.

These data will be useful in three ways: (1) deciding whether chemical composition varies between species, (2) determining the quantities of phosphorus in the biomass of higher organisms, and (3) determining the annual loss of phosphorus from the sea through the harvest of fishery products.

Chemical Analysis

The organic phosphorus in the dried or partially ashed (8 hr at 500–600°C) specimen was converted to inorganic forms by a sulfuric-nitric acid digestion. After digestion the residue was fumed down to about half its volume to reduce a by-product of the digestion reaction, nitrosyl sulfuric acid. This was necessary to prevent interference from the by-product in the subsequent phosphorus analysis. The sample was cooled and a portion of it diluted to the equivalent of about 10,000 ml per gram dried sample weight. Two sets of aliquot samples were prepared for analysis. One contained 1 ml of the diluted specimen mixture and the second, 3 ml. The samples of both sets were diluted to 25 ml with distilled water. The analytical method employed was that described by Robinson and

Thompson (1948). Control samples were prepared from KH_2PO_4 and also from a dried powdered fish mixture of known phosphorus composition. The purpose of the latter was to detect interference due to the nitrosyl sulfuric acid in the samples. Each specimen was analyzed four times. The precision of the average of the four analyses per specimen was estimated to be 0.1 mg P per gram sample weight (dry basis). The analyses are tabulated in Table 1.

TABLE 1

Phosphorus content of certain fishes and shrimp

Species	No. of specimens	Average weight		Per cent of phosphorus		
				Wet weight	Dry weight	
		Wet g	Dry g	Average	Average	Standard deviation
Lanternfish (Family Myctophidae)	34	1.2	0.26	0.82	3.11	0.37
Searobin *Prionotus tribulus*	12	7.2	1.89	0.84	3.20	0.71
Broad killifish *Cyprinodon variegatus*	24	1.1	.26	0.70	3.08	0.33
Spot *Leiostomus xanthurus*	14	35.6	7.94	0.51	2.29*	0.36
8-fingered threadfin *Polynemus octonemus*	22	4.2	0.78	0.55	3.00	0.70
Catfish *Galeichthys felis*	10	20.7	4.85	0.82	3.49	0.27
Ling *Phycis floridanus*	22	46.8	8.99	0.47	2.43	0.24
Anchovy *Anchoviella mitchilli*	19	.....	0.06	.....	2.91	0.24
Mullet *Mugil cephalus*	16	20.5	5.10	0.83	3.31	0.49
Mullet *Mugil cephalus*	15	.....	0.04	.....	2.53	0.25
Menhaden *Brevoortia patronus*	14	27.0	6.72	0.80	3.39	0.66
Menhaden *Brevoortia patronus*	19	0.7	0.13	0.76	3.81	0.54
Shrimp—Male *Penaeus setiferus*	7	22.7	5.41	0.36	1.49	0.09
Shrimp—Female *Penaeus setiferus*	17	23.7	5.64	0.34	1.41	0.27
Shrimp (sex unknown) *Penaeus setiferus*	25	.....	1.44	.....	1.47†	0.34

* Phosphorus analyses performed on "ashed" samples.
† Phosphorus analysis of 10 specimens was performed on "ashed" samples.

Discussion

We were not able to find any reference to phosphorus data, based on the entire animal, of the species we analyzed. However, analyses of entire organisms have been reported for other species. Sempolowsky (1889), cited in Atwater (1892), reported phosphorus contents of 0.53 and 0.78%, based on the entire fish, for the haddock (*Melanogrammus aeglefinus*) and the gray gurnet (*Trigla gurnardus*). Weigelt (1891), cited in Vinogradov (1953), reported 0.52–0.56% and 0.45–0.51% (whole weight basis), respectively, for the same species, 0.36% for the sea herring (*Clupea harengus*), 0.57–0.61% for the cod (*Gadus morrhua*), and 0.43% for the anglerfish (*Lophius piscatorius*). We

are aware of only one study of fresh-water fish in which the entire animal was analyzed for phosphorus. McCay *et al.* (1931) in nutritional studies of fresh-water trout (*Salvelinus fontinalis*) reported a range of 0.24–0.55% based on the entire fish.

Milone (1896), cited in Vinogradov (1953), reported a substantial decrease in phosphorus content with size for two species that he analyzed. The phosphorus content of Mediterranean species (*Smaris vulgaris*) was 0.53 and 0.89% (whole weight basis) for large and small specimens, respectively. Similarly, he reported values of 0.34 and 1.10% (whole weight basis) for the surmullet (*Mullis surmuletus*). Analysis of the menhaden (*Brevoortia patronus*) and shrimp (*Penaeus setiferus*) data (Table 1) shows no significant difference in the phosphorus content of large and small specimens. There appears to be a significant difference, however, in the phosphorus content of the two groups of mullet (*Mugil cephalus*).

The higher phosphorus content of fish as compared to shrimp was undoubtedly due to the high phosphate content of bone. The bones of many fish contain up to 65% mineral residue (Roche and Bullinger 1939), the $Ca_3(PO_4)_2$ content of which has been reported as high as 94% (Vinogradov 1953). Fish scales from some species also contain large amounts of phosphorus. Carnot (1893) was cited by Vinogradov (1953) as having reported values as high as 98.38% as $Ca_3(PO_4)_2$ for the mineral content of certain scales. The phosphorus content of the soft parts of fishes averaged about 0.3% on a whole weight basis (Vinogradov 1953), but variation among species is quite large. Krukenberg (1877) was cited by Vinogradov (1953) as having reported 0.032% for the dogfish (*Acanthias vulgaris*), and Javillier and Cremieu (1928) report 0.93% for the carp (*Cyprinus carpio*). This variation may reflect results based on individual specimens rather than on the mean of a number of fish (Vinogradov, 1953).

Shrimp show (Table 1) little difference in phosphorus content between sexes or size groups. The values shown (1.41–1.49%) are somewhat higher than that of Decapoda, in general, which range from 0.63–1.36% on a dry weight basis (Vinogradov, 1953). Again, we were unable to make a direct comparison with work on *Penaeus setiferus*. Weigelt (1891), cited in Vinogradov (1953), reported a value of 1.27% (dry weight basis) for *Crangus vulgarius*, and Delff (1912), also cited in Vinogradov (1953), reported 1.08% for the same species.

It is not the purpose of this paper to delve into the biogeochemical aspects of phosphorus, other than to mention that the phosphorus content of marine animals constitutes an important source for the return of this element to the land. Hutchinson (1952) stated that based on Clark's (1889) estimate, approximately 13.7 million tons of phosphorus are delivered to the oceans annually. The biogeochemical paths of return are considerably less than this (Hutchinson, 1952), and as a result, phosphorus at the surface of land masses may be decreasing. Hutchinson (1952) stated that the annual return of phosphorus to the land by fisheries of the world, based on an annual catch of 25–30 million tons, is about 60,000 tons. The estimate would assume an average phosphorus value of about 0.25% which is considerably less than the values shown in Table 1. We therefore believe his estimate to be conservative.

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Chaetognatha From the Texas Coast

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Abstract

Three genera and eleven species of chaetognaths were identified from collections made in the bays and along the Texas coast. No marked difference was noted between the faunas of the west coast of Florida and the Texas coast. Other studies show the same species of chaetognaths present along the coast from Cape Hatteras around the Gulf and extending into Central American waters. *Sagitta tenuis*, *S. enflata*, and *S. hispida* were most numerous.

Introduction

The chaetognath fauna of only a limited area of the Gulf of Mexico has been investigated. Although chaetognaths have been reported from the west coast of Florida and Cuba, (Ritter-Zahony 1910, Pierce 1951, 1954, Suarez-Caabro 1955, and Tokioka 1955) there are no published reports on the Chaetognatha of the Texas coast. Not only does the Texas coast represent a very large area, but the interruption in the inshore salinity pattern produced by the Mississippi River poses a question concerning the similarity of arrow worms of the coastal waters of the eastern and of the western Gulf.

During the summer of 1960, I had the opportunity of collecting plankton samples in a number of places in the Port Aransas area of Texas. As a result of a short trip to Veracruz, Mexico, during the same summer, I secured two more samples far down the Mexican coast. Also I was fortunate to obtain 62 plankton samples collected by Mr. E. D. McRae when he was employed in 1951 by the Texas Game and Fish Commission Marine Laboratory at Rockport, Texas. As a result of the 107 samples reported in this paper, the general pattern of the distribution of chaetognaths along portions of the Texas coast is apparent.

Methods

A variety of nets was used in making these collections. These included a Clarke-Bumpus Sampler and a 10 and a 16-inch net. Several types of netting were used but all were fine enough to retain very small chaetognaths. Most of the samples were collected in shallow water with oblique tows from near bottom to the surface. Tows were usually of 10 to 30 minutes duration. Salinity samples were taken and salinity determinations made by titration with silver nitrate.

Plankton tows were made in the small bays north and south of Aransas Pass as seen in Fig. 1. The northernmost tows were in Copano and Aransas Bays just a few miles north of Aransas Pass. The southernmost tows were off Port Isabel near the Mexican border. Two collections were made off Veracruz, Mexico, from an area where no chaetognaths had been reported within 500 miles (see insert, Fig. 1)

[1] Visiting lecturer in NSF sponsored Advanced Subject Matter Institute in Marine Science at Port Aransas in 1960.

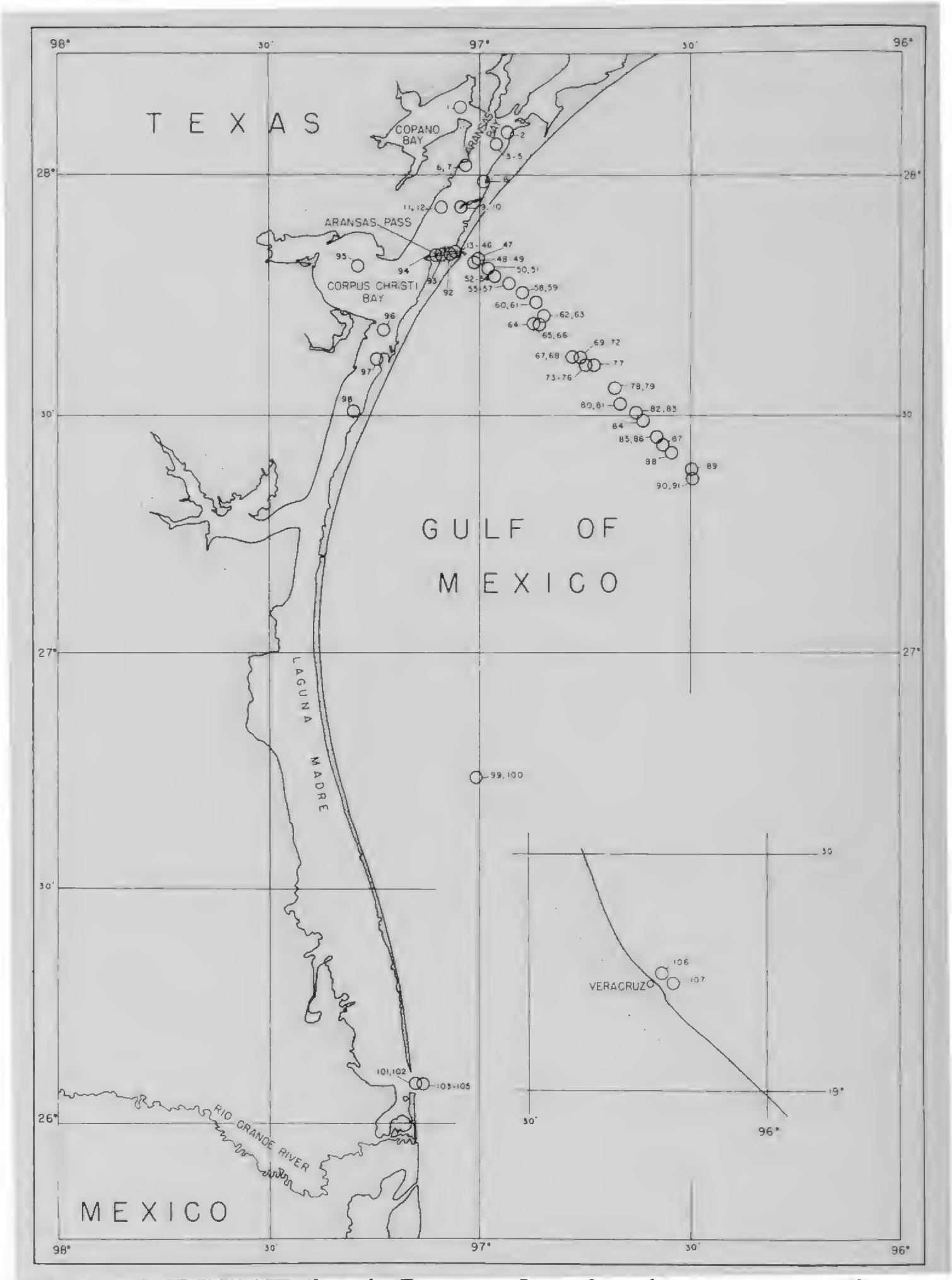

FIG. 1. Collecting stations along the Texas coast. Insert shows the two stations near Veracruz, Mexico.

Results

Three genera and eleven species of chaetognaths were collected along the Texas coast. The genera included *Sagitta* with eight species, *Krohnitta* with two species, and *Pterosa-*

gitta with one species. These species are shown in Table 1 in order of decreasing abundance.

TABLE 1

Chaetognaths collected along the Texas coast

Species	No.	Bays 19 samples		Aransas Pass 34 samples		Coast 54 samples	
		Times collected	Per cent times collected	Times collected	Per cent times collected	Times collected	Per cent times collected
S. tenuis	5190	8	42	34	100	45	83
S. enflata	1674	0	0	19	56	40	74
S. hispida	385	4	21	8	24	22	41
S. minima	191	0	0	1	3	12	21
K. pacifica	145	0	0	2	6	23	43
S. serrato	105	0	0	0	0	13	23
P. draco	16	0	0	0	0	5	9
S. helenae	10	0	0	3	9	4	7
S. lyra	6	0	0	0	0	1	2
S. bipunctata	4	0	0	0	0	2	4
K. subtilis	2	0	0	0	0	1	2
Total	7728						

Sagitta tenuis was the most abundant and the most widespread. 5190 specimens were found in all the samples. This species was present in 42% of the bay samples, 100% of the Aransas Pass samples, and 83% of the samples taken along the coast. It occurred in water of salinities ranging from 29.1 to 39.7 ‰. Its apparent reduced incidence in the bays is partly the result of four samples taken in Corpus Christi Bay and the Laguna Madre which yielded no chaetognaths of any kind. In the northern section of the Laguna Madre (Fig. 1) where the samples were taken, the salinities ranged from 45.6 to 51.6 ‰. Plankton generally was reduced, but not absent from these samples. The high salinity appeared to be the responsible factor for the absence of chaetognaths. If this is true, it points to an upper limit of salinity which these species do not tolerate in nature.

Specimens of *S. tenuis* collected in this study agree in general morphological detail with individuals deposited in the U.S. National Museum by F. S. Conant who described the species (1896). There do not appear to be enough distinctive features in these specimens to warrant separating them into two species. Admittedly in view of the systematic problems involved in the separation of *S. tenuis* and *S. friderici* comparative studies of specimens from widely spaced localities are needed.

S. enflata was second in abundance, although absent in the bays and clearly most abundant off the coast in stations 47 to 91. It was found in salinities ranging from 31.9 to 37.2 ‰, but clearly its optimum habitat is the saline offshore water (Pierce 1951, 1953, and 1958).

S. hispida is typically an inhabitant of bays and inshore water (Pierce 1951 and 1958). It was the only other species found with *S. tenuis* in the bay waters. It occurred in reduced numbers in many of the stations located a number of miles from shore. Its presence offshore can in part be explained by the strong outflow of water from Aransas Pass. The salinity range of 31.6 to 37.2 ‰ in the coastal water where *S. hispida* was collected indicates appreciable dilution at times by bay water.

S. helenae, eighth in abundance, occurred commonly along the coast and extended outward over the continental shelf (Pierce 1951, 1958, Bumpus and Pierce 1955). It was common along the Gulf and Southeastern Atlantic coasts.

The other species, *S. minima, S. serratodentata, S. lyra, S. bipunctata, K. pacifica, K. subtilis,* and *P. draco,* are customarily found over the outer portion of the continental shelf (Pierce 1953, Bumpus and Pierce 1955, and Owre 1960) and across the oceans. These have all been collected in the shelf and ocean waters off the coast of the southeastern Atlantic states. These species were almost entirely absent from both bay and pass water. Their occurrence in these samples is in agreement with other records of their distribution.

Association of Species

Selected samples are tabulated in Table 2 to show the relative abundance and association of the chaetognaths found in bay, pass, and coastal waters. In the bays, *S. tenuis* or *S. hispida* occurred in reduced numbers. In any one sample there were usually but a few

TABLE 2

Selected samples from bays, Aransas Pass, and coastal waters illustrating typical associations and relative abundance of species.

Chart station*	Date	Salinity ‰	Location	Species			
2	7 March, 1951	32.0	Aransas Bay	7	*S. tenuis*		
15	7 July, 1960	37.0	Aransas Pass	3	*S. enflata,*	56	*S. tenuis,*
				1	*S. hispida*		
32	19 July, 1960	32.6	Aransas Pass	19	*S. enflata,*	12	*S. tenuis*
49	12 April, 1960	32.9	Coast, 2 mi. S.E. entrance Aransas Pass	91	*S. hispida,*	4	*S. tenuis*
58	30 July, 1951	36.3	Coast, 9 mi. S.E.	3	*S. enflata,*	42	*S. tenuis,*
			entrance Aransas Pass	1	*S. helenae,*	6	*K. pacifica,*
				20	*S. hispida*		
75	20 July, 1951	36.5	Coast, 21 mi. S.E.	21	*S. enflata,*	5	*S. hispida,*
			entrance Aransas Pass	3	*S. serrato,*		
				18	*S. tenuis*		
90	1 August, 1951	36.3	Coast, 40 mi. S.E.	1	*S. bipunctata,*	3	*S. serrato,*
			Aransas Pass	27	*S. enflata,*	2	*K. pacifica,*
				27	*S. minima,*	11	*P. draco*
100	3 August, 1951	36.5	Coast, 17 mi. E.	6	*S. enflata,*	2	*S. tenuis,*
			Laguna Madre	1	*S. hispida,*	5	*K. pacifica*
			26°4′ N., 97°01′ W.				
101	3 August, 1951	.....	Coast near entrance to Port Isabel	3	*S. hispida,*	20	*S. tenuis*
107	19 July, 1960	.....	Coast, 12 mi. S.E.	4	*S. enflata,*	20	*S. tenuis,*
			Veracruz, Mexico	1	*S. hispida*		

* Stations can be located in Figure 1.

members of either species. Aransas Pass samples commonly contained both *S. hispida, S. tenuis,* and occasionally *S. enflata.* The presence of the last species indicates an influx of offshore water in the pass. The absence of *S. serratodentata* and *S. bipunctata* is a strong indication that only a limited amount of offshore water was introduced into the pass during the period when these samples were taken.

The group of species characteristic of the offshore Gulf water included *S. bipunctata, S. lyra, S. minima, S. serratodentata, K. pacifica, K. subtilis,* and *P. draco.* Few of this group appeared in samples closer than six miles to Aransas Pass. As shown at stations 53, 75, and 90 in Table 2, most of these appeared together in many of the offshore stations.

Temperature and Salinity

During the summer of 1960, temperatures close to 30°C. were usually recorded in the surface waters of the bays, passes, and coastal water. From the limited data available, there is no indication what effect temperature may have on distribution along the coast of Texas, nor are the precise effects of salinity clear. The high salinity of the Laguna Madre (45 to 51 ‰) did appear to prevent chaetognaths from living there as none at all were found in the four samples from this area. In the remainder of the samples, salinities of several parts per thousand both below and above 35 ‰ were encountered in the bay, pass, and coastal waters. The fact that many of the samples were taken in areas of shallow water and strong tides probably masked the effect that salinity might have exerted had there been a chance to observe stabilized salinity concentration in such places.

Discussion

There does not appear to be any striking difference in the distribution of chaetognaths between the eastern and western portions of the Gulf of Mexico. *S. hispida* and *S. tenuis* are common inshore species in Florida and Texas. *S. helenae* appears to be more abundant along the west coast of Florida than along the Texas coast. Since this species occurs principally in the waters over the continental shelf, the wider shelf off the west coast of Florida may be a factor favoring a larger population there.

More extensive studies have been published on the arrow worms off the Southeastern Atlantic states (Pierce 1953, 1958, Bumpus and Pierce 1955, and Owre 1960). These report the presence of the same species under conditions comparable to the Texas coast. North of Cape Hatteras the chaetognath fauna changes abruptly. South of Cape Hatteras, over the continental shelf from North Carolina to Texas, there does not appear to be any marked change in the distribution of chaetognaths.

The two samples taken off Veracruz, Mexico, indicate that this same fauna extends along the Mexican coast. Moreover, Suarez-Caabro and Madruga (1960) recorded the presence of *S. hispida, S. tenuis, S. enflata,* and other species off Honduras. All of the species collected by Surez-Caabro were present along the Texas coast. It is now apparent that the coastal water south from Cape Hatteras, the Gulf of Mexico, Cuba, and portions of Central America support a similar chaetognath fauna.

Acknowledgments

I am indebted to Dr. Howard T. Odum, Director of the Institute of Marine Science, for allowing me the use of laboratory facilities and a collecting boat at Port Aransas, and to Mr. Howard Lee, Director of the Texas Game and Fish Commission Marine Laboratory at Rockport, for the use of his facilities. Miss Karen Hodges, my assistant for the summer of 1960, was most helpful in the sorting and enumeration of many of the chaetognaths reported in this paper.

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An Ecological Survey of the Lower Laguna Madre of Texas, 1953-1959[1]

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Abstract

Hydrographic data and annotated comments on the distribution and habits of species are presented for the Lower Laguna Madre of Texas, a shallow, hypersaline marine bay extending 76 miles north of the Rio Grande delta. In summer, waters of the Gulf move northward through the lagoon with increasing salinity due to evaporation. The variety of species in the plankton and bottom communities diminish with distance from the pass. In winter, flow is southward. A population of commercial oysters, *Crassostrea virginica*, near the pass apparently is adapted to high salinity conditions. Some ecological effects of man-made changes are described, including the effects of opening Port Mansfield Pass, the isolation and silting of South Bay due to spoil, and the management of the Rio Grande River during floods. Movements of year classes of game fishes are described.

Introduction

The Laguna Madre of Texas (Fig. 1) is a generally shallow, hypersaline bay area on the South Texas coast extending from Corpus Christi Bay south to the Rio Grande River. This bay has long been important in commercial fisheries production and in recent years, with the general decline in commercial production of other areas of the coast, has become the leading producer of such important bay fishes as the black drum, redfish, and the spotted trout. Since World War II, this area has also become important to bay sports fishing.

This report concerns an ecological survey made in the Lower Laguna Madre from September of 1953 to September of 1959. For the purpose of comparison, an effort was made to follow as closely as possible the general outline and reporting procedure used in two previous papers on other sections of the Laguna Madre: *An Ecological Survey of the Upper Laguna Madre of Texas* (Simmons, 1957) and *An Ecological Survey of Baffin and Alazan Bays, Texas* (Breuer, 1957). Regular collections were made at thirteen stations (Fig. 1)including representative habitats and depths. Data are presented on hydrography, species, fish mortalities, and effects of the Port Mansfield Pass.

Previous Investigations

There have been few investigations in the Lower Laguna Madre area. Daugherty from 1948 to 1950 initiated preliminary investigations at Port Isabel, and Miles continued these investigations from 1951 to 1952 and reported on fish movement and migrations. Whitten, Rosene and Hedgpeth (1950) reported on the invertebrate fauna of the Brazos Santiago jetties. Carlgren and Hedgpeth (1952) described several anthozoans from Brazos Santiago Pass, Port Isabel, and South Bay. Hedgpeth (1953) discussed com-

[1] Contribution No. 50 from the Marine Laboratory, Texas Game and Fish Commission, Rockport, Texas.

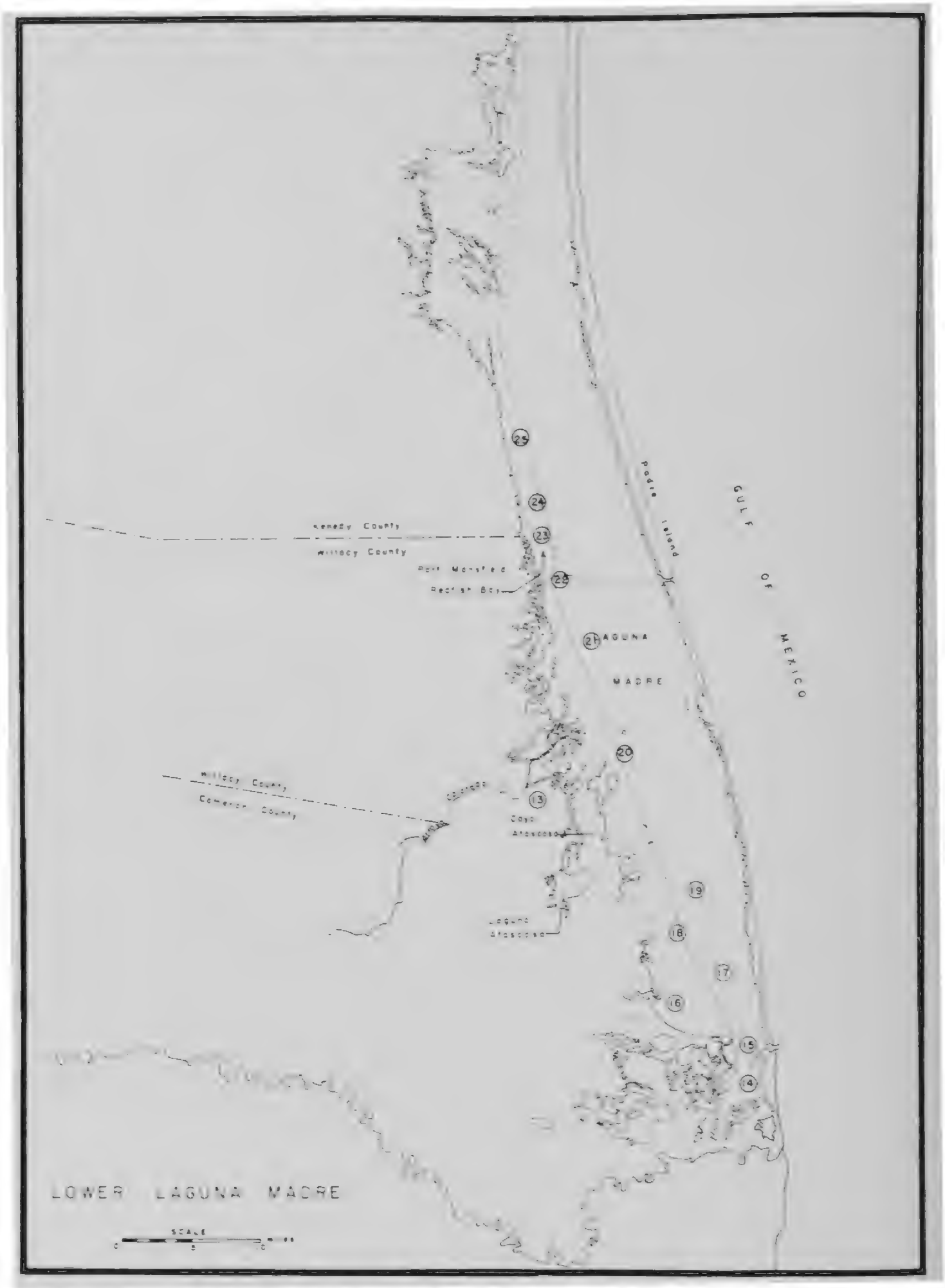

FIG. 1. Lower Laguna Madre of Texas, with principal sampling stations, Nos. 13–25.

munity relationships in South Bay. Shepard and Rusnak (1957) and Rusnak (1960) mapped the bay sediments and described other geological features. Parker (1959) contributed significant knowledge on the macroinvertebrate assemblages of the area. Other literature of value to the completion of this study included Burkenroad (1951), Collier

and Hedgpeth (1950), Gunter (1950), Hedgpeth (1950), and Simmons and Breuer (1962).

Description of Area

The Lower Laguna Madre (Fig. 1) is located on the south Texas coast from a point 11 miles north of the southern boundary of Kenedy County south to the Rio Grande, an air-line distance of about 74 miles. It is bounded by Padre and Brazos Islands on the east and by the Texas mainland on the west. The lagoon is bisected by the Intracoastal Canal from the northern end south to Port Isabel. The Brownsville Ship Channel extends from the jetties of Brazos Santiago Pass which separates Padre and Brazos Islands, west to Port Brownsville. Natural islands are abundant near the Arroyo Colorado delta, but many are surrounded by mud flats.

The Lower Laguna Madre area can be divided into four parts (Fig. 1). The northern-most area, Redfish Bay, (not to be confused with Redfish Bay near Port Aransas) extends from the landlock or land-cut south to approximately four miles south of Port Mansfield. The middle area extends from this point south to Three Islands. The area known as Port Isabel Bay extends from Three Islands south to the Brownsville Ship Channel. South of this channel is South Bay.

With changing water levels due to wind variations, there is no sharp demarcation between land and water. For the purpose of describing land and water areas, U.S. Coast and Geodetic Survey charts 896, 897, and 898 were used. These charts show yellow for land, blue and white for water, and green for flat lowland often inundated by water. See Fig. 2.

In the northern end of the bay there is severe filling due to encroachment of sand from the island (Fig. 3). Filling in at the landcut is complete, and the entire bay area is composed of shallow flats, subject to inundation only at times of high water. These extend west from Padre Island 1 to 2½ miles from the northern extreme of Redfish Bay south to Three Islands. From Three Islands south to Brazos Santiago Pass, these flat, exposed areas are less than one-fourth mile in width.

Along the mainland shores, the boundary of land and water is definite in the Redfish Bay area. The mainland is semi-arid pasture land with many oak motts. Water depths of over one foot extend to within a few yards of shore. There are considerable areas of flats subject to inundation along the mainland shore of the entire middle portion due to deltas built up by the North Floodway, Arroyo Colorado, and the Cayo Atascosa. The mainland shores of Port Isabel Bay are well-defined, as are those of Redfish Bay. The South Bay area is surrounded by exposed flats resulting from siltation from the Rio Grande and dredge spoil from the Brownsville Ship Channel.

Water area of Redfish Bay is about 53,000 surface acres, which is normally covered by water. About one-third of this area, or 18,000 acres, is six feet deep or more at mean low tide. This deep water forms a long, narrow, irregular patch paralleling the shore some 13 miles through Redfish Bay. The Intracoastal Canal was dredged through this deep water, but the resulting spoil banks are submerged and have little influence on water transport in the area. This deep water, along with the absence of substantial spoil banks, causes this area to be quite rough in either north or southeast winds.

The middle area contains some 47,500 water acres. With the exception of the Intracoastal Canal, there is no water over three feet in depth, and the average is closer to one foot.

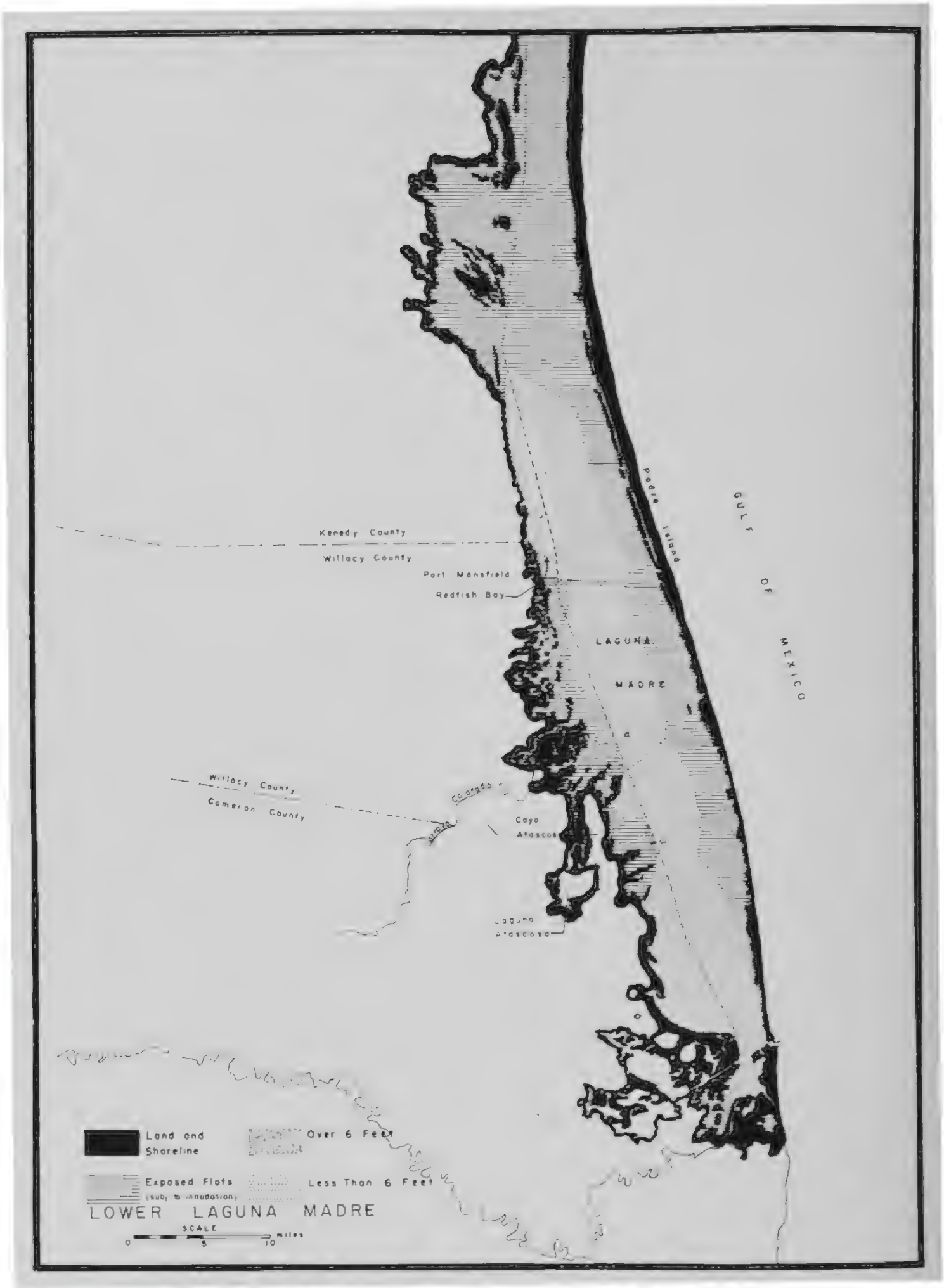

FIG. 2. Depth and distribution of flats in the Lower Laguna Madre.

The Port Isabel Bay area (Fig. 4) contains another 47,500 acres of water, although the average depth is from three to four feet, much more than the middle area. The only sections with depths greater than six feet, with the exception of the Intracoastal Canal

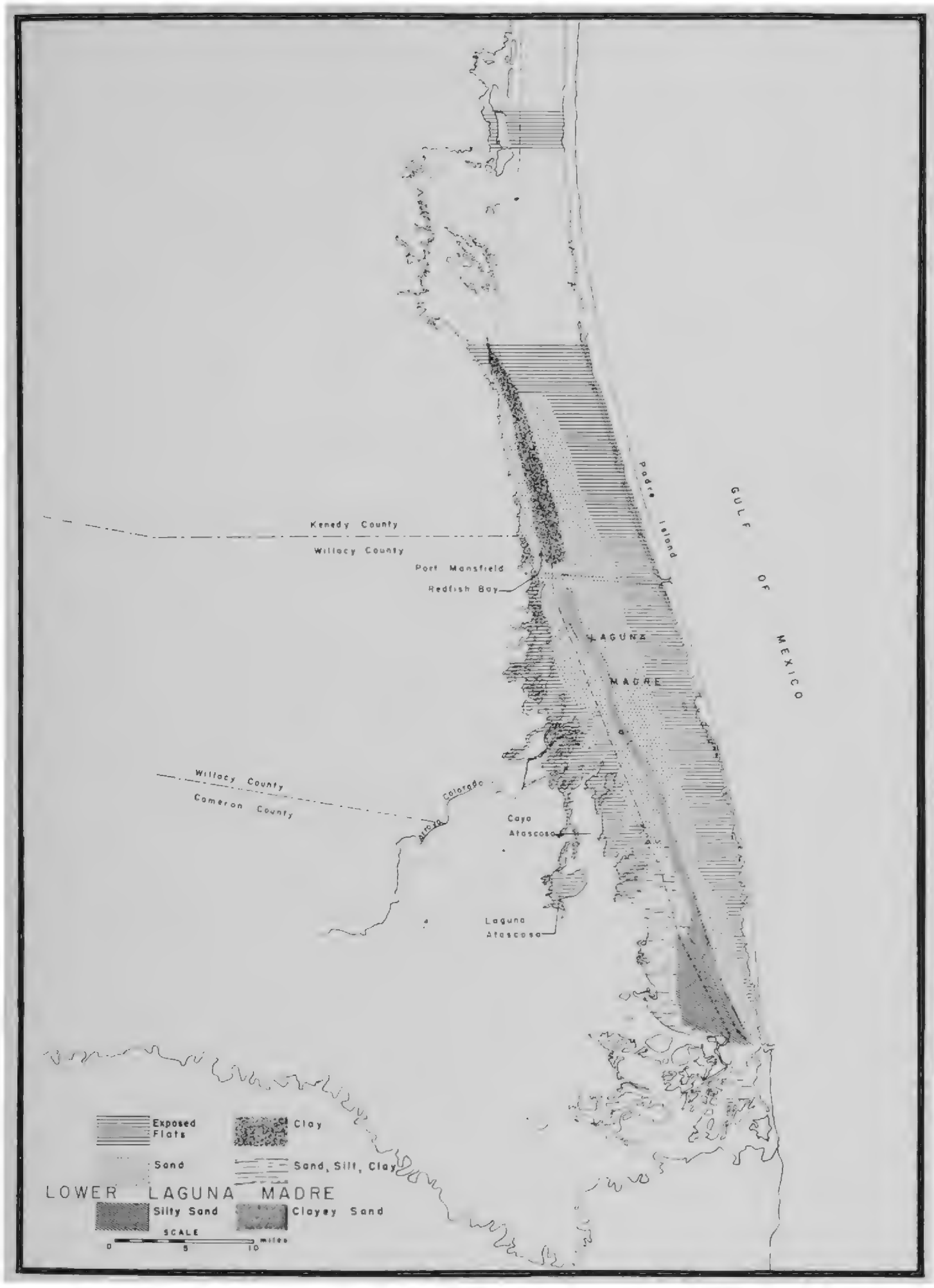

FIG. 3. Type of sediments in the Lower Laguna Madre after Shepard and Rusnak (1957).

and the Brownsville Ship Channel, are several areas in the vicinity of the Queen Isabella Causeway and the Padre Island Coast Guard Station.

South Bay at present contains some 2,500 surface acres of water with a maximum depth of three feet and an average of 18 inches.

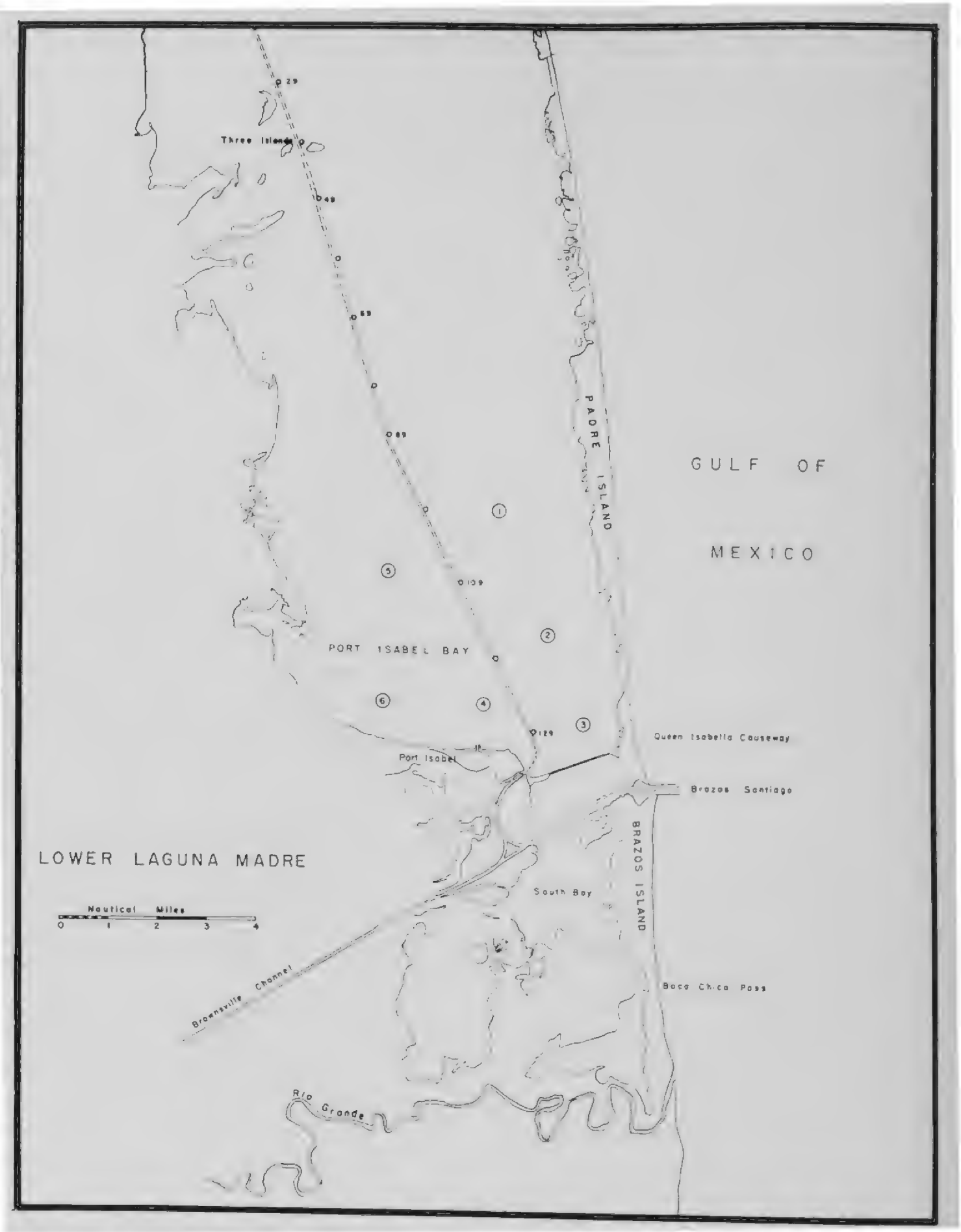

FIG. 4. Map of the Lower Laguna Madre in the vicinity of the Brazos Santiago Pass. Numbers in circles are experimental oyster reefs.

The Intracoastal Canal, extending 63 miles from Port Isabel to the landcut, has a bottom width of 125 feet and is 12 feet deep. The Brownsville Ship Channel is fifteen miles long, extending from Brazos Santiago Pass to Brownsville, and is from 100 to 1,000 feet wide and 36 feet deep. The approach to this channel through the pass is 300 feet wide and 38 feet deep. The twenty-five miles of dredged Arroyo Colorado, opening Port Har-

lingen, is 125 feet wide and nine feet deep. The five miles of channel connecting Port Mansfield with the Gulf of Mexico is 100 feet wide and 12 feet deep.

From Port Mansfield south to Three Islands, the mainland shore is of a delta-type built up in the past by flood outlets of the Rio Grande. These waterways are now known as the North Floodway, Arroyo Colorado, and Cayo Atascosa. From Three Islands south to Port Isabel, the mainland shore is again well-defined. Two hundred years ago an arm of the Rio Grande emptied into South Bay. Since then, the river has changed its course to empty into the Gulf of Mexico. Boca Chica Pass was closed by nature, with considable help by man, at the south.

The North Floodway, which empties into the Laguna Madre about fourteen miles south of Port Mansfield, normally carries drainage from much of the Rio Grande Valley. Excess rainwater and irrigation water is drained from the land via this floodway. The volume of water carried is normally very low.

The Arroyo Colorado is also a floodway and carries drainage and excess rainwater from other portions of the watershed. Both the North Floodway and the Arroyo Colorado connect with the Rio Grande near Mission, Texas, and can carry flood waters from the Rio Grande when this river reaches flood stage.

The Cayo Atascosa also carries drainage and irrigation water into the bay. The Atascosa Wildlife Refuge impounds most of this water, however, and seldom does any reach the bay. The Cayo empties into the Arroyo Colorado about two miles west of the Intracoastal Canal.

There is no other source of fresh water stream flow into the bay area. In fact, except in times of flooding, the amount of drainage into the Lower Laguna Madre must be considered negligible.

History

Prior to 1935, with the exception of Port Isabel Bay, the Lower Laguna Madre was a primitive area known mainly by commercial fishermen. Port Mansfield, Arroyo City, Holly Beach, Laguna Vista, Intracoastal Canal, the dredged Arroyo Colorado, the Atascosa Wildlife Refuge, the Naval Air Station, Brownsville Ship Channel, Port Brownsville, Queen Isabella Causeway, and the Cameron County Park on Padre Island did not exist.

In 1948 the Intracoastal Canal was dredged from Corpus Christi Bay to Port Isabel. This waterway provided a safe boat route for the entire length of the Laguna, and sports fishing increased. With Port Isabel as the terminus of the intracoastal waterway and the Brazos Santiago Pass as an outlet into the Gulf of Mexico, the Brownsville Navigation District completed the deep-water channel fifteen miles inland to form the new Port of Brownsville. The Cameron County Navigation District dredged the Arroyo Colorado from the Intracoastal Canal, through Rio Hondo, and at its terminus built the Port of Harlingen. Willacy County formed a Navigation District, built Port Mansfield and connected it with the Intracoastal Canal. Recently a channel and pass were dredged to the Gulf, and jetties have been constructed on the Gulf entrance.

In spite of these modifications, the Lower Laguna Madre remains largely an unpopulated bay area. Most of the adjoining land is owned or controlled by government or large private concerns such as the King Ranch, U.S. Fish and Wildlife Service, and the U.S. Navy.

Hydrography

Circulation and Salinity

Data on salinities obtained by the author, at stations in the Lower Laguna Madre (Fig. 1) are presented in Table 1. Data on wind and rainfall, obtained from the records of the Weather Bureau, U. S. Department of Commerce, are given in Table 2. Some discussion of the distribution of wind and rainfall provides an explanation for the salinity distribution.

Table 1

Salinities in the Lower Laguna Madre in ‰

Date	Stations												
	13	14	15	16	17	18	19	20	21	22	23	24	25
June, 1954	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
July, 1954	3.2	34.5	35.2	36.6	35.8	39.1	40.5	40.6	37.7	34.0	39.0	40.7	42.7
August, 1954	.....	35.0	34.7	36.4	.....	.....	.....	.....	41.5	42.0	41.1	43.7	44.3
September, 1954	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
October, 1954	5.1	32.2	28.5	33.7	33.7	33.5	29.8	27.9	38.4	40.0	39.9	43.5	43.0
December, 1954	11.5	33.2	33.2	.....	32.5	.....	33.5	.....	39.0	41.1	45.1	48.8	51.1-W
February, 1955	9.6	36.8	34.8	36.6	.....	36.5	35.3	.....	37.3	40.0	42.8	48.7	52.1-W
May, 1955	14.0	35.0	36.0	40.0	43.0	42.0	43.0	.....	48.0	46.0	48.0	48.0	55.0
June, 1955	.....	13.4	35.5	35.7	38.6	36.2	.....	.....	39.8	44.6	44.5	44.4	45.2
August, 1955	9.8	41.3	39.0	41.0	39.6	42.8	44.6	44.2	46.8	45.2	47.2	47.4	47.8
September, 1955	.....	39.5	30.0	26.1	.....	23.5	.....	.....	29.2	24.9	25.5	25.1	27.0
November, 1955	.....	36.2	35.8	42.5	30.1	31.7	28.8	.....	23.4	25.0	28.3	28.4	29.0
January, 1956	.....	38.1	35.6	31.9	32.2	31.1	31.1	23.3	35.3	32.1	37.1	28.7	39.5
March, 1956	6.6	35.1	35.6	35.4	35.4	39.1	36.4	34.0	35.0	32.4	36.6	39.2	40.6
June, 1956	10.4	37.7	.....	40.6	35.2	35.4	.....	21.9	41.0	40.6	41.6	41.4	42.2
August, 1956	20.8	.....	38.5	41.4	.....	44.5	44.0	47.0	47.2	47.5	.....	.....	.....
September, 1956	16.9	39.1	38.3	41.1	41.4	43.9	43.7	41.4	42.1	46.6	.....	.....	.....

Table 2

Wind and rainfall at Raymondville, Texas

Month	Prevailing wind			Rainfall inches
	Direction	Frequency per cent	Mean velocity, mph	
September, 1953	NW	13	10.3	0.35
October, 1953	ESE	22	10.6	1.95
November, 1953	SE	12	10.1	3.46
December, 1953	NW	17	12.5	0.84
January, 1954	SE	25	12.9	0.26
February, 1954	SSE	17	13.0	0.09
March, 1954	SSE	28	15.6	0.55
April, 1954	SE	39	16.1	4.07
May, 1954	ESE	31	14.1	2.27
June, 1954	SE	47	15.3	2.87
July, 1954	SE	40	11.8	0.21
August, 1954	SE	31	11.6	1.27
September, 1954	SE	15	9.3	4.05
October, 1954	SE	20	9.2	3.74
November, 1954	NW	17	10.8	1.69
December, 1954	SE	18	10.6	0.11
January, 1955	SE	18	12.2	1.58
February, 1955	SE	24	14.2	0.37
March, 1955	SSE	31	16.2	0.03
April, 1955	SE	27	15.4	0.16
May, 1955	SE	42	15.7	5.61

TABLE 2—Continued

Wind and rainfall at Raymondville, Texas

Month	Prevailing wind			Rainfall inches
	Direction	Frequency per cent	Mean velocity, mph	
June, 1955	SE	39	13.6	0.30
July, 1955	SE	34	11.3	4.03
August, 1955	SE	29	9.8	2.79
September, 1955	E	17	9.5	15.90
October, 1955	SE	15	9.6	1.16
November, 1955	SSE	24	13.7	0.63
December, 1955	NNW	15	10.9	0.57
January, 1956	SSE	15	11.6	0.03
February, 1956	SSE	23	14.9	1.23
March, 1956	SE	27	14.0	.....
April, 1956	SE	22	14.8	4.32
May, 1956	SE	43	15.2	2.76
June, 1956	SE	43	12.9	1.05
July, 1956	SSE	41	14.4	0.04
August, 1956	SSE	33	13.9	1.20
September, 1956	S	17	8.4	2.21
October, 1956	SSE	11	8.0	0.64
November, 1956	SSE	18	13.3	0.47
December, 1956	SSE	19	9.8	1.00
January, 1957	SSE	32	15.0	0.05
February, 1957	SE	18	13.0	2.55
March, 1957	SSE	24	15.1	2.57
April, 1957	SE	33	16.9	3.23
May, 1957	SE	44	16.1	2.14
June, 1957	SE	37	13.5	4.66
July, 1957	SE	44	13.5	0.56
August, 1957	SE	34	12.4	0.30
September, 1957	SE	17	12.1	1.50
October, 1957	SE	17	13.0	1.30
November, 1957	SE	17	13.9	3.48
December, 1957	SE	21	13.0	0.11
January, 1958	NW	20	12.9	7.33
February, 1958	SE	18	13.3	3.91
March, 1958	SE	19	12.2	0.71
April, 1958	SSE	27	13.5	0.23
May, 1958	SE	17	9.9	1.77
June, 1958	SE	32	12.6	2.17
July, 1958	SSE	42	12.3	3.27
August, 1958	SSE	37	11.4	.....
September, 1958	SE	13	9.3	4.44
October, 1958	NW	21	10.5	10.94
November, 1958	NNW	16	9.4	1.80
December, 1958	NNW	30	10.6	1.25
January, 1959	NNW	18	10.6	1.44
February, 1959	NNW	19	11.0	2.69
March, 1959	SSE	17	11.8	0.13
April, 1959	SSE	25	11.7	1.20
May, 1959	SE	38	13.0	2.15
June, 1959	SSE	30	11.0	1.43
July, 1959	SSE	35	10.0	0.46

The Intracoastal Canal extending the entire length of the Lower Laguna Madre, along with the opening to the Gulf of Mexico at Brazos Santiago Pass at the south, and the opening through the land-cut to the Upper Laguna Madre to the north, provides principal water exchange. It is this circulation that prevents excessive hypersalinity. Current direction varies with the seasons. During the summer months, the prevailing wind is from the south and southeast. These prevailing winds, along with the south-to-north shore cur-

rent in the Gulf, cause the water of the Gulf to enter the bay area through Brazos Santiago Pass, flow north through the entire Lower Laguna Madre and through the land-cut to the Upper Laguna Madre area. During the winter months, the prevailing wind is from the north, and the entire situation is reversed. South and southeast winds prevail through most of the year, however, and the resulting current affords excellent water exchange in the area. However, the water entering the system is from the Gulf of Mexico, with a salinity of 32 to 35 ‰, and not fresh river water. The freshest water in the Lower Laguna Madre, proper, is adjacent to Brazos Santiago Pass. The salinity gradually increases as the water travels north. Highest salinities encountered are at the northern end of Redfish Bay. During the summer, salinity variations from the two ends of the system may be as high as 15 ‰, due to the heavy rate of evaporation. This variation is somewhat less in the spring and fall because of the lower evaporation rates.

Extremely high rate of evaporation in the landlock and Upper Laguna Madre during the summer and fall months causes a high salinity in these waters. The prevailing northerly winds during the winter months bring this hypersaline block of water south into Redfish Bay. Thus, the highest salinity in the upper Laguna appears in August, (Simmons, 1957) while in the lower Laguna it is in February (Table 1). In both cases, hypersalinity is due to lack of adequate circulation, extensive areas of shallow water, and the high rate of evaporation in the Upper Laguna Madre area.

The newly completed channel and pass from Port Mansfield to the Gulf of Mexico has had some effect on water currents in the area. The project was completed in 1958, using patented concrete tetrapods for jetty construction. By 1959, a bar had built up between the jetties, making the pass no longer navigable, although it remained functional until July of 1960, when the pass was purposely closed to facilitate construction of new impervious jetties. At this writing, jetties and channel dredging are complete, with the opening of the pass occuring in May, 1962.

The effect of the pass, while open, on the currents of the area has already been established. In the prevailing souheast wind, the water enters the Brazos Santiago Pass through a minimum cross-section of 43,200 sq. ft., and the water leaves the area through a land-cut with a minimum cross-section of 3,600 sq. ft. These measurements were taken from the U. S. Corps of Engineers plans and specifications. The Port Mansfield Pass provides a valve for the head of water built up in Redfish Bay. The current flows out from bay to Gulf. Only during periods of north winds, and the resulting north-to-south current, is the situation reversed (numerous personal observations). The prevailing current, then, through the two passes, is exactly opposite. The pass at Port Mansfield stabilizes the salinity in the Redfish Bay area.

Tidal Effects

The high set of the Gulf in the spring and fall causes the water level of the area to rise sharply from 12 to 18 inches. The water level also varies with the diurnal tides and is most noticeable at Port Isabel. The daily effect, however, decreases away from the pass, or to the north. These tides may complement the steady current. An incoming wind current in Port Isabel Bay can be very swift or slow, depending on whether the tide is coming in or out. As one travels north, the effect of tide on current becomes less noticeable. The effect at Three Islands is slight, and at Port Mansfield, is negligible. No correlation exists between temperature and any other hydrographical or meteorological factors,

other than salinity through rate of evaporation. Evaporation is greater during the months when temperatures are the highest and the days longest; higher salinities result. Since higher temperatures exist in the summer months, the variation in salinity from Brazos Santiago Pass to the land-cut is greater during these months.

The Arroyo Colorado and North Floodway are both flood control overflows for the Rio Grande. These are seldom used since the great dams have been built in the Rio Grande. In the fall of 1958, these two channels carried an estimated 5,000,000 acre feet of water into the bay fromt he flooding Rio Grande, which otherwise would have caused great destruction in Brownsville and other Valley cities. This influx of fresh water greatly affected the bay area, and its effect was noted for at least 6 months. Species normally confined to the brackish Arroyo Colorado, such as threadfin herring and alligator gar, were present in the bay, proper. For example, salinity at Three Islands in August, 1958, was 35.6 ‰. After the flooding, salinities dropped to 13.2 ‰ in November, 1958, rose to 17.4% in December, and to 31.2% in April of 1959.

Turbidity of the waters of the Lower Laguna Madre varied considerably, and observations made in the study seem consistent with the following interpretations of the role of wind, current, tide, water runoff, depth of water, and bottom type. The most important factor was the presence or absence of bottom vegetation. Water overlying a bottom devoid of vegetation was seldom clear, such as the deeper waters of South Bay; and a bottom with heavy growth of submerged vegetation was seldom turbid, such as in the Green Island-Three Islands area. In general, turbidity in shallow water was observed to be caused by wind; in deeper water, by current and tide. Runoff from the surrounding watershed was found to be turbid if the flow was heavy, as evidenced by the flooding in the fall of 1958. Turbidity was greater in waters over a silt or clay bottom, such as in the area at the old mouth of the Arroyo Colorado. Turbidity was less over a sand bottom, as along the bay side of Padre Island (Shepard and Rusnak, 1957). In general, the waters of South Bay were very turbid over barren bottoms, but clear among heavy submerged vegetation, as observed on numerous occasions. Water also was unusually clear between the Brownsville Ship Channel and Queen Isabella Causeway, where there was heavy vegetation, in spite of the strong currents. Water was also clear from the Causeway north to Three Islands between the Intracoastal Canal and Padre Island. In addition, there were other small areas of comparatively low turbidity.

Salinity and Species Variety

Among the bay fishes, the number of species present increases and the number of individuals of each species decreases, as the salinity of the bay water approaches Gulf salinity, either from a fresh or from a hypersaline condition. This is true of invertebrates and vegetation as well. The greatest number of floral and faunal species is found at the approach to the Brazos Santiago Pass, for here, both Gulf and bay forms are interspersed.

As the distance from the pass is increased, and the salinity deviates from Gulf salinity, the number of species decreases, but the total number of individuals of the remaining species increases. Details are cited in the following annotated list.

Annotated Notes on Occurrence of Species

Although far from complete, the listings that follow provide a synopsis of some of the biota during the study period, 1953–1959.

Some of the literature used, which was valuable in the identification of species, was Humm and Caylor (1957), Freese (1952), Hartman (1951), Gunter (1945), Pearson (1929), Ladd (1951), and U.S. Department of Interior (1954).

Plants

Almost all of the plants are relatively dormant during the winter months. Brown and red algae begin to appear in February. The grasses start to show growth in March. Maximum growth for all types appears in June and July. The decay of algal forms and the defoliation of the grasses coincide with the high water temperatures of August and September.

All of the red and brown algae of the area are found south of Three Islands in salinities of less than 40 ‰. *Cymodocea manatorium* and *Thalassia testudinum* also occur in South Bay and in the vicinity of Port Isabel at or near Gulf salinity.

In spite of the strong bay current capable of carrying all Gulf plankton forms throughout the entire bay system, most species of diatoms were found near the pass. Some genera such as *Stephanopyxis, Rhizosolenia, Chaetoceros, Fragilaria,* and *Thalassiothrix* were found only near Brazos Santiago Pass. There were exceptions, such as *Licmophora, Nitzschia,* and *Coscinodiscus,* which were found at all stations. *Navicula* was most common in brackish waters. The salinity range in this area apparently did not affect the dinoflagellates.

The following list is incomplete, as identifications of prepared slides and microphotographs are incomplete. The species listed in the Chlorophyta, Phaeophyta and Rhodophyta are from a single incidental sampling, identified by Dr. E. Yale Dawson, Allan Hancock Foundation, University of Southern California, and do not purport to be a complete list of algae for the area.

Phylum Chrysophyta
Class Bacillariophyceae
Order Centrales

Hemidiscus sp. Rare at station 15.

Stephanopyxis palmeriana (Greville) Grunow. Rare at station 15 in January.

Melosira sp. Rare at station 15.

Coscinodiscus sp. Found at all stations, apparently more common in Port Isabel Bay. Least abundant in summer.

Rhizosolenia sp. Common at stations 14 and 15 near Brazos Santiago Pass during summer months.

Chaetoceros sp. Found abundant only in January at stations 14 and 15 near the pass.

Biddulphia sp. Taken only at stations 14 and 15 at all times, but never abundant.

Order Pennales

Fragilaria crotonensis (A.M. Edwards) Kitton. Rare, found at station 14 in August.

Nitzschia sp. Scattered over most stations from March through May, not abundant.

Striatella sp. Found from South Bay to Port Mansfield, most common in north Port Isabel Bay in August.

Licmophora sp. Found from March through August at most stations, common at station 17 in August.

Thalassiothrix sp. Common at station 14 in March.

Asterionella japonica Cleve. Very common in Gulf surf at Brazos Island in September.

Thalassionema nitzchiodes Grunow. Taken in Brazos Santiago Pass in May.

Synedra sp. Station 15 in February.

Gyrosigma sp. Station 14 in March.

Pleurosigma sp. Station 14 in March.

Phylum Chlorophyta

Enteromorpha flexiosa J. Agardh. Common near Port Isabel.

Ulva sp. Common near Port Isabel.

Cladophora sp. aff. *C. dalmatica* Kutzing. Common in Arroyo Colorado in late spring.

Acetabularia crenulata Lamarck. Found throughout the area attached to marl and dead shells.

Phylum Phaeophyta

Dictyota cervicornis Kutzing. Found in Port Isabel Bay in summer months.

Sargassum sp. Entered passes in spring months; common then in Port Isabel Bay, Port Mansfield Pass, and on Gulf beaches.

Phylum Rhodophyta

Hypnea cervicornis J. Agardh. Common at stations 15 and 16.

Corallina granifera Ellis & Solander. Taken in Port Isabel Bay in late spring.

Gracilaria blodgettii Harvey. Very common from Port Isabel to Three Islands from April to September.

Phylum Spermatophyta

Cymodocea manatorum Aschers. "Manatee grass," a dark green, reed-like grass common in the Port Isabel area in the vicinity of Brazos Santiago Pass.

Diplanthera (Hadoluli) wrightii Aschers. "Shoal grass" was present to some extent over almost all of the Laguna Madre area, the most common and abundant vegetative type.

Ruppia maritima Linneaus. "Widgeon grass" was found along the Intracoastal Canal from Three Islands north to Port Mansfield and in the old bed of the Arroyo Colorado.

Halophila engelmanni Aschers. This small plant was found sparingly with *Diplanthera* in the Three Islands-Green Island area. Characteristically there are three pairs of leaves at the apex of the branch.

Thalassia testudinum Konig. "Turtle grass," in vast meadows, occurred in South Bay interspersed with *Cymodocea manatorum*, both north and south of Queen Isabella Causeway.

Phylum Protozoa
Class Mastigophora
Order Dinoflagellidia

Dinoflagellates occurred at all stations at all times of the year, although never in large numbers. All species were found throughout the area, most abundant near passes.

Peridinium depressum Bailey.

Ceratium fuscus (Ehrenberg) Du Vardin.

Ceratium macroceros (Ehrenberg) Vanhoffen.

Certatium tripos (O. F. Müller) Nitzsch.

Ceratium furca (Ehrenberg) Du Vardin.

Phylum Porifera

Numerous sponge specimens have been collected near the mouth of Brazos Santiago Pass, but no identifications have been made at this time.

Phylum Coelenterata
Class Hydrozoa
Order Hydroida

Nemopsis bachei L. Agassiz. Common in winter months throughout the entire area.

Eudendrium sp. The specimens collected were examined by C. E. Cutress of the Smithsonian Institution and reported by him to be an unknown species, probably new to science.

Aglaophenia late-carinata Aldmann. This hydroid was common, attached to floating Sargassum weed.

Class Scyphozoa
Order Rhizostomeae

Stomolophus meleagris Agassiz. The "cabbage head" was found occasionally in the Port Isabel area but was not nearly so common as in other areas of the Texas coast.

Order Semaeostomeae

Aurelia aurita (Linnaeus). Fairly common throughout the area, more prevalent during winter months.

Class Anthozoa
Order Actiniaria

Much more work is needed on this order, particularly on forms associated with the oyster reefs, jetties, and sea walls in the Port Isabel area. Hedgpeth reported *Anthopleura krebsi* as the common form on the Brazos Santiago jetties.

Calliactis tricolor (LeSueur). Common on the sea walls at Port Isabel and attached to large shells.

Paranthus rapiformis (Le Sueur). Two specimens taken by shrimp trawl at the base of Brazos Santiago jetties, adjacent to Brownsville Ship Channel.

Order Madreporaria

Astrangia sp. Several living colonies have been found attached to the submerged concrete pilings of the Queen Isabella Causeway at Port Isabel. This coral has been very common on the north jetty at Brazos Santiago Pass. Skin divers have taken hundreds of heads, since the spring of 1960, ranging in size from that of a golf ball to that of a basketball.

Phylum Ctenophora

Beroë ovata Chamissa and Eypenhardt. Very young specimens taken during late winter and early spring, adult specimens common in summer.

Phylum Annelida

Branchiomma nigromaculata (Baird). Represents an extension of range for the species. Dr. Olga Hartman states that *B. nigromaculata* has not been recorded from the western part of the Gulf. This species was common among the oysters of the Port Isabel area.

Nereis pelagica occidentalis Hartman. This polychaete was common among oyster clumps as well as in other parts of this area. This bright red worm becomes an active surface swimmer at night, especially during the summer months, and will come to a bright light at night. They are readily taken as food by small fish.

Phylum Arthropoda

Class Crustacea

Order Copepoda

All species not otherwise noted were taken from Brazos Santiago Pass.

Acartia lilljeborgi Giesbrecht.

Acartia tonsa Dana. Most abundant of all copepod species, found at all times and at all stations, withstands high salinities and has been found in almost fresh water.

Anomalocera ornata Sutcliffe.

Calanopia americana Dahl.

Centropages furcatus (Dana).

Clausocalanus furcatus (Brady).

Eucalanus pileatus Giesbrecht.

Labidocera scotti Giesbrecht.

Labidocera aestiva Wheeler.

Macrostella sp. Rare throughout the area.

Metis holothuriae (Edwards)=(*M. jousseaumei* Richards). Most common at station 25 in summer months.

Oithona brevicornis Giesbrecht. Rare throughout the area.

Paracalanus aculeatus Giesbrecht.

Paracalanus crassirastris Dahl.

Paracalanus parvus (Claus).

Pontellopsis villosa Brady.

Temora stylifera (Dana).

Temora turbinata (Dana).
Tisbe sp.
Tortanus sp.

Order Cirripedia

Balanus eburneus Gould. The "ivory barnacle" was found wherever there was a place for attachment.
Balanus amphitrite Darwin. More common in lower salinity waters near Brazos Santiago Pass.
Lepas pectinata Spengler. Found on floating sargassum weed.

Order Isopoda

Nerocila acuminata Schioedte and Meinert. Parasitic in the mouths of croakers (*Micropogon sp.*).
Probopyrus pandalicola Packard. Parasitic on gills of *Palaemonetes intermedius.*

Order Amphipoda

Amphipods were very common throughout the entire area, but little work has been done with them at this time. They were found among dead and living grasses, and algae, as well as among barnacles and oyster clumps.
Elasmopus sp. Common among green algae.
Grubia compta (Smith). Common among green algae.
Caprella sp. Rare in plankton samples near Port Isabel, a different species common on the brown algae of Brazos Santiago jetties.

Order Decapoda

Penaeus setiferus (Linnaeus). The white shrimp was rare in most areas of this region, but a large population was present from June to September in a shallow, almost enclosed, water area immediately north of the junction of the Arroyo Colorado and the Intracoastal Canal, immediately west of the spoil banks at Intracoastal Canal marker 324. South Bay and the Arroyo Colorado were frequently used as a summer nursery grounds for this species of shrimp.
Penaeus aztecus Ives. The brown shrimp was present throughout the entire area at all times, but was very scarce during winter months. The middle area was an important nursery grounds. Although it does not reach sufficient size for table use in this area, this shrimp provides a basic food for the spotted trout and the southern flounder.
Penaeus duorarum Burkenroad. The pink shrimp was found in the summer months, interspersed with the brown shrimp in the Port Isabel area, particularly near the Brownsville Ship Channel. Apparently it cannot tolerate as high a salinity as *P. aztecus* and has not been found north of Three Islands.
Palaemonetes intermedius (Holthuis). Very common throughout the area, found among the green algae of the Arroyo and among shoal grass in the Laguna, tolerant of both high and low salinities and temperatures. One female specimen, which was

doubly infected with *Probopyrus pandalicola* Packard (one in each gill chamber), was taken, apparently a rarity.

Crangon heterochaelis (Say). The pistol shrimp was found among the oyster clumps of Port Isabel and was common along the south and west shore of Port Isabel Bay. This shrimp appeared to be abundant on the shallow flats in the Three Islands area, as evidenced by its presence in the stomachs of the redfish *Sciaenops ocellatus* (Linnaeus) taken there.

Tozeuma carolinensis Kingsley. Found in Port Isabel Bay during the summer months.

Pagurus sp. Not numerous, but found near the Brownsville Ship Channel.

Hepatus epheliticus (Linnaeus). Scarce, a few strays near the jetties at Port Isabel.

Calappa flammea (Herbst). Also rare, but occasionally entered the approach to the Brazos Santiago jetties.

Callinectes sapidus Rathbun. Very common in the juvenile stages during the spring months. Adults were present throughout the entire area during the summer, with males present all year.

Callinectes danae Smith. The Gulf crab was the predominant portunid in the vicinity of Brazos Santiago Pass and in South Bay.

Neopanope texana (Stimpson). Mud crab, very common in the vicinity of Three Islands.

Uca sp. Fiddler crabs were common in the low-lying areas near the bay.

Pinnotheres ostreum Say. The oyster crab was common near Port Isabel. The female was found living commensally in commercial oysters in the area.

Metoporhaphis sp. Spider crabs were taken periodically by trawl near Brazos Santiago jetties.

Libinia sp. As in the species above.

Order Stomatopoda

Squilla sp. Mantis shrimp were taken in trawl drags in the Port Isabel area during the summer months.

Phylum Mollusca

Many species of molluscs were represented in the area only by the presence of their dead shells. Where the live animals of these species were not found, they are not listed here. Other species which are not listed are those Gulf forms which were accidentally and temporarily introduced into the bay area. Pulley (1952) and Abbott (1954) were valuable in the identification of these species.

Class Amphineura
Order Polyplacophora

Several chitons have been collected from the Port Isabel area, but most have not yet been identified.

Chaetopleura apiculata (Say). Common among the experimental oyster reefs of Port Isabel Bay.

Class Pelecypoda

Brachidontes exustus Linnaeus. Common on oyster clumps in the Port Isabel area.

Aequipecten irradians amplicostatus Dall. Very common from Three Islands south in the spring months, apparently migratory.

Anomia simplex d'Orbigny. Common on inner surfaces of dead oyster shells.

Crassostrea virginica (Gmelin). Common in South Bay and commercially harvested there, also present in quantities at Queen Isabella Causeway, Port Isabel. There were deposits in other scattered areas in the Port Isabel area. This population may be a new physiological race, as it not only tolerated, but spawned and achieved rapid growth, in salinities in excess of 40 ‰.

Special attention was given to the commercial oyster population centered in South Bay, the only sizable concentration of oysters south of Corpus Christi, and unique in many ways. South Bay was almost totally lacking in water circulation. Water depth averaged 18 inches and was usually very turbid. The bottom was of soft mud to which other layers were added yearly by nearby dredging. Water temperatures ranged to both extremes, and salinities remained steady at 32 to 42 ‰.

In spite of these seemingly adverse conditions, limited oyster production has continued for 25 years. In spite of the limited cultch, spatfall seemed to be more than adequate. Spawning, while occurring daily in spring and fall, continued throughout the year, as shown by the presence of all sizes of spat and seed oysters at any given time. A percentage of the total adult population were in an edible condition throughout the year, as indicated by the year-round commercial harvest. Most landings occurred in summer when commercial oyster harvest was prohibited by law in the main oyster producing areas of the state.

The study of South Bay oysters has given rise to a developmental project now underway. In April of 1958, six quarter-acre oyster reefs were built in Port Isabel Bay (Fig. 4). Each reef was made by depositing a six-inch deep layer of mud shell, using 300 cubic yards for each reef. Three of these reefs were then seeded, each with 200 bushels of South Bay seed oysters (Reefs 2, 5, and 6).

The purpose of the experiment was to determine whether these oysters would do as well in the seemingly more favorable environment of Port Isabel Bay as in South Bay. The experimental reef areas were vastly different from South Bay in type of bottom, water depth, temperature extremes, siltation, and water circulation. Salinity was essentially the same in both areas.

Results of this study are far from complete. A sudden prolonged reduction in salinity in the area in October and November of 1958 caused high mortality among both seed oysters and spat. Some seed oysters managed to survive the reduced salinity, showing a salinity tolerance of at least 1.4 ‰ to 42.0 ‰ since planting. Young oysters of all lengths from 4 to 90 mm were present at all times, indicating a somewhat continuous spawning. Growth to 90 mm on spat collectors has been attained in one year on several reefs during 1958. At the present time, these reefs are most valuable as fishing reefs; their future as producers of commercial oysters is in doubt.

Ostrea equestris Say. Very common in the Port Isabel areas, especially near the jetties and along the base of the causeway. The main spatfall of the horse or gulf oyster, *Ostrea equestris*, occurred in April and May, 1958. This oyster was more abundant on the reefs nearest Brazos Santiago Pass; it was almost unknown in South Bay. Seeded reefs contained a higher percentage of commercial oysters (*Crassostrea*) than the unseeded reefs at this time. Mortality occurring during a period of decreased salinity was greater among the horse oysters than among the commercial oysters.

Polymesoda floridana Conrad. Found throughout the bay area but not abundant.
Laevicardium mortoni Conrad. Present over much of the bay bottom, fairly common.
Anomalocardia cuneimeris Conrad. Found from Three Islands north to the land cut.
Chione cancellata Linnaeus. Common during spring and summer months from Three Islands south to the Brownsville Ship Channel.
Mercenaria campechiensis Gmelin. A few specimens remain in South Bay. This species was harvested commercially before the dumping of spoil for the Brownsville Ship Channel dredging. Other live specimens have been found in the vicinity of experimental oyster reef 4.
Tagelus gibbus (Spengler). Found along the Brownsville Ship Channel.
Ensis minor Dall. Fresh dead shells common throughout the area.
Mulinia lateralis (Say). Found from Three Islands north. Used as food by the black drum along with *P. floridana, L. mortoni,* and *A. cuneimeris.* No large deposits of any of these have been found to date.
Pholas (Barnea) costata Linnaeus. The angelwings were common in a few areas at Port Isabel.
Congeria (Mytilopsis) sallei Recluz. Very abundant for a short time only during the summer of 1956 in the Arroyo Colorado, absent before and since.

Class Gastropoda

Order Prosobranchia

Neritina virginea (Linnaéus). Common among shoal grass on south shore of Port Isabel Bay.
Littorina ziczac Gmelin. Very common on the jetties at Brazos Santiago Pass.
Littorina nebulosa Lamarck. The angulate periwinkle was found on pilings near Brazos Santiago Pass and in the Port Isabel basin.
Littorina irrorata Say. The marsh periwinkle was found adhering to grass and reeds near Port Isabel and along the Brownsville Ship Channel.
Cerithium variabile C. B. Adams.
Cerithidea pliculosa Menke. Rare, south of Three Islands.
Epitonium sp.
Crepidula plana Say. Common in the Port Isabel area.
Murex fulvescens Sowerby.
Thais haemostoma floridana Conrad. Very common on the Brazos Santiago jetties.
Anachis avara semiplicata Stearns.
Nassarius vibex Say. Common in Port Isabel Bay.
Pleuroploca gigantea (Kiener). Found under Queen Isabella Causeway.

Order Opisthobranchia

Suborder Tectibranchia

Tectibranchs are fairly common in the summer months in the Port Isabel area. In addition to those listed here, three other species have been collected but not yet identified.
Bulla occidentalis C. B. Adams. Rare in Port Isabel Bay.
Bursatella leachi pleii (Rang). The ragged sea hare, a blue green in color, was taken at Station 15 during the summer months by trawl, a new record from Texas.

Aplysia (Tethys) willcoxi Heilprin. The mottled sea hare was common at Port Isabel, a new record from Texas.

Aplysia (Tethys) dactylomela Rang. Larger than *A. willcoxi* and with black rings, common.

Aplysia (Tethys) floridensis Pilsbry. Uniform purple black color, rare with only one specimen taken until the summer of 1959 when over 100 specimens were sighted in Brazos Santiago Pass.

Order Pulmonata

Siphonaria lineolata d'Orbigny. Common on the Brazos Santiago jetties.

Class Cephalopoda

Order Decapoda

Loligo brevis Blainville. Fairly common near the Queen Isabella Causeway during the summer months and rare in South Bay during the winter months.

Phylum Echinodermata

Class Ophiuroidea

Several unidentified species are common on the oyster clumps of Port Isabel.

Class Echinoidea

Arbacia punctulata (Lamarck). Found south of Queen Isabella Causeway, but not common.

Lytechinus variegatus (Lamarck). Common at Station 15 in late spring and early summer.

Mellita quinquesperforata (Leske). A few specimens taken just inside the Brazos Santiago jetties. The young were very common just past the surf on the Gulf beach in June.

Class Crinoidea

Crinoid material was taken from under the Queen Isabella Causeway, but no identifications have been attempted as yet.

Class Holothuroidea

Thyonella sabanillensis (Deichmann). Several specimens were taken adjacent to Brownsville Ship Channel just inside jetties.

Order Apoda

Synaptula hydriformis (LeSueur). Very common east of Intracoastal Canal from Queen Isabella Causeway to Three Islands in summer.

Phylum Ectoprocta

Class Gymnolaemata

Membranipora tuberculata (Bosc). Common on sargassum weed near Port Isabel.

Phylum Chordata

Order Selachii

Sharks were very common at the end of the Brazos Santiago jetties and along the Gulf beach including the Hammerhead, *Sphyrna zygaena* (Linnaeus), Bonnethead, *Sphyrna tiburo* (Linnaeus), and the sand shark *Carcharhinus sp.*
Sharks were seldom seen or caught inside the pass.

Order Batoidei

Pristis sp. The sawfish has been reported at Port Isabel, but none were taken in the survey work.

Raja sp. Oystermen in South Bay report skates, but none were taken in the survey.

Dasyatis sabina (Le Sueur). The stingaree was common in South Bay, at the base of the Brazos Santiago jetties, and north to the mouth of the Arroyo Colorado, but rare from there north.

Aetobatus narinari (Euphrasen). Two specimens were seen near the Queen Isabella Causeway, not common.

Rhinoptera bonasus (Mitchill). Several schools were seen in the Intracoastal Canal near Green Island apparently migrating. Several specimens were reported caught near Three Islands on trot lines, not common.

Order Lepisosteida

Lepisosteus productus Cope. Spotted gar.

Lepisosteus spatula (Lacépède). Alligator gar as well as spotted gar were common in the brackish and fresh waters of the area, such as the Arroyo Colorado and floodway systems. In times of low salinity, they entered the bay for a period.

Order Nematognathi

Bagre marinus (Mitchill). The gafftopsail catfish was taken occasionally in the Port Isabel area but was not common.

Galeichthys felis (Linnaeus) the sea catfish (hardhead) was very common throughout the area, especially in the deeper waters of the channels. Male catfish carrying eggs ready for hatching were found at Station 13 on June 22, 1954.

Order Isospondyli

Tarpon atlanticus (Cuvier and Valenciennes). The tarpon was a popular sports fish in the lower Port Isabel Bay area, as well as in the Brazos Santiago Pass. It was common during the summer months north to Three Islands and in the Arroyo Colorado.

Elops saurus Linnaeus. The tenpounder was fairly common, especially in waters of lower salinity.

Dorosoma cepedianum (Le Sueur). The gizzard shad was present in the Arroyo Colorado and North Floodway, rare elsewhere.

Brevoortia gunteri (Hildebrand). The bay menhaden was fairly common in the entire bay area.

Brevoortia patronus Goode. A few specimens of the Gulf menhaden were taken in the Port Isabel area as far north as Three Islands. Both species used the Arroyo Colorado as nursery grounds.

Anchoviella sp. Very common from Three Islands north to the landlock, and very abundant during winter months, it was the most plentiful bait fish in the bay during December and January.

Order Iniomi

Synodus foetens (Linnaeus). A few specimens were taken near the Brazos Santiago jetties, not common.

Fundulus grandis (Baird and Girard).

Fundulus pulvereus (Evermann).

Cyprinodon variegatus Lacépède. All three were common in the shallow fresh and brackish waters of the area, North Floodway and Laguna Atascosa.

Order Synentognathi

Strongylura marina (Walbaum). The needlefish was present throughout the area but much more common in the deeper water of the Intracoastal Canal during the summer months.

Order Solenichthyes

Syngnathus sp. Pipefish were very common in trawl drags throughout the bay area.

Hippocampus sp. An occasional adult sea horse was taken at Station 15. Young were common in the manatee grass in South Bay.

Division Acanthopterygii

Menidia beryllina peninsulae (Goode and Bean). The tidewater silverside was common in the area but more abundant in summer in the less saline waters. It replaced the anchovy of more saline waters.

Mugil curema Cuvier and Valenciennes.

Mugil cephalus Linnaeus. Both the striped and white mullet were common throughout the area, particularly in the Arroyo Colorado and the Intracoastal Canal. Juvenile forms were found in the Arroyo in December and January.

Polydactylus octonemus Girard. The eight-fingered threadfin was present but not common and was most abundant along the Brownsville Ship Channel.

Scomberomorus maculatus (Mitchill). The Spanish mackerel was common in the Gulf waters adjacent to shore during the spring and summer months, and a few individuals occasionally entered the bay area.

Scomberomorus cavalla (Cuvier and Valenciennes). The king mackerel usually was found slightly farther offshore than the Spanish mackerel, but clear water in close to shore brought these fish in almost to the beach. Some specimens have been taken from the jetties but not as often as the Spanish mackerel.

Trichiurus lepturus Linnaeus. The cutlass fish was a common resident of the Intracoastal canal during the summer from Port Isabel to the mouth of the Arroyo.

Caranx hippos (Linnaeus). The adult common jack, an offshore species, has not been taken in the bay, but juveniles of the species were taken near the jetties.

Caranx crysos (Mitchill). Hardtail jack were relatively common near the jetties and causeway.

Vomer setapinnis (Mitchill). The moonfish was common along the Gulf beach and the jetties.

Chloroscombrus chrysurus (Linnaeus). The bumper, which commonly travels with schools of menhaden, was occasionally seen near the jetties. A few specimens entered the bay.

Selene vomer (Linnaeus). The lookdown was common along the Gulf beach in the summer months in company with the moonfish.

Trachinotus carolinus (Linnaeus). The common pompano was a regular resident of Port Isabel Bay during the spring and summer months, especially from the Queen Isabella Causeway northwest to Port Isabel and north to Three Islands and Port Mansfield.

Peprilus alepidotus (Linnaeus). The harvestfish was commonly taken by hook from the jetties by sportsfishermen in the spring and early summer.

Poronotus triacanthus (Peck). The butterfish was also common at the jetties and was taken along with the harvestfish.

Centropomus undecimalis (Bloch). The snook, or pike as it is known locally, was common during the warmer months at the mouth of the Rio Grande. In winter it was readily taken by spoons and plugs in the deep waters of the Brownsville Ship Channel.

Mycteroperca sp.

Epinephelus sp. Several species of young grouper not yet identified have been taken by trawl at Station 15 during late spring and early summer.

Promicrops itaiara (Lichtenstein). The spotted jewfish was a common resident of the "caves" under the Brazos Santiago jetties as well as in the sunken ships and other submerged wrecks. The young have not been found.

Lobotes surinamensis (Bloch). The triple-tail was found in the summer months from the jetties north to Three Islands, usually floating on its side beneath rafts of dead shoal grass, sargassum weed, or floating lumber.

Lutjanus sp.

Lutjanus apodus (Walbaum). The schoolmaster and other snappers were common at Station 15 from April to July.

Haemulon sp.

Orthopristis chrysopterus (Linnaeus). The pigfish, highly prized as bait for large spotted trout, was not too common in the area. Most specimens have been taken in the Port Isabel area.

Lagodon rhomboides (Linnaeus). The pinfish was very common throughout the entire area. It was tolerant of a wide range of salinity and temperature. In this area, the pinperch constituted a large percentage of the diet of the spotted trout and was used as live bait for trot lines.

Archosargus probatocephalus (Walbaum). The sheepshead was quite common in the Port Isabel area, especially under piers and docks, although large schools have been seen in the open bay as far north as Port Mansfield. In January, large schools

of sheepshead were common in Redfish Bay, and the young (30–50 mm) were present at Three Islands.

Eucinostromus gula (Cuvier and Valenciennes).

Eucinostromus californiensis (Gill). Both the common and Gill's mojarra were abundant in the area, but no attempt was made to separate species after initial identification.

Cynoscion arenarius Ginsburg.

Cynoscion nothus (Holbrook). Both species of sand trout have been taken at Port Isabel near the approaches to the jetties. Neither was common in the area and seldom were they found far into the bay proper.

Cynoscion nebulosus (Cuvier and Valenciennes). The spotted seatrout was common to the entire area and sought after by both the sports and commercial fishermen. They were present throughout the year and were taken on trot lines baited with live perch, piggies, with plastic, by spoons, plugs, or shrimp.

Juvenile trout were found among beds of dense shoal grass in many areas of the bay. Nursery grounds were extensive throughout the area except in Port Isabel Bay and in South Bay.

Adult trout were found throughout the bay in the warmer months but were confined to the deeper waters of the bay and channels during the coldest months. Many trout were taken with spoons and live shrimp from the jetties or Gulf surf during winter months, indicating a migration to the gulf of some of the trout popultaion during the coldest weather. Tagging results indicate that trout which wintered in the Arroyo Colorado spent the summer months in the grassy areas along the intracoastal canal from Three Islands to the Cameron-Willacy County line. Trout in the Redfish Bay area were believed to follow the brown shrimp migration north to the land cut in early spring.

Prior to 1955, juvenile brown shrimp were the most important food item in the diet of smaller trout (1 to 3 pounds). Since that time, however, the use of the swarming nocturnal polychaete, *Nereis pelagica occidentalis* Hartman as food by these trout has increased considerably, especially along the intracoastal canal from Port Mansfield to Three Islands. This shift in food preference and the resulting change from daytime to night time feeding has resulted in decreased daytime trout catches, since it appears that this trout population does not feed with equal vigor both day and night. Experimental net catches made in the mornings revealed a sizable trout population with stomachs full of polychaete worms. This change in feeding time was quickly noted by the sports and commercial fishermen, who began fishing with live shrimp in the channels at night under batteries of lights. These lights attracted large numbers of shrimp, small fish, crabs, and worms which, in turn, attracted the trout. This method has become the most reliable way of catching large numbers of trout in this area.

Large sow trout, ranging from 8 to 14 pounds, were common to the area but did not appear on the sports stringer in sufficient numbers to indicate their presence in the area. Live shrimp was the most popular trout bait in the region, but did not bring in large fish for trout over eight pounds were fish eaters, feeding primarily on mullet, skipjack, pinperch, piggies, and other trout. Indications of the large sow trout population in the area were given by experimental netting, illegal net landings, fish kills, and trot line landings when fish were used for bait.

Bairdella chrysura (Lacépède). The silver perch, locally called "yellow tail" was com-

mon in the Arroyo Colorado and the Port Mansfield channel. Both young and adult have been taken adjacent to the Brownsville Ship Channel in late winter.

Stellifer lanceolatus (Holbrook). The star drum was common in the Gulf in three to five fathoms but seldom entered the bay area.

Sciaenops ocellatus (Linnaeus) the channel bass (redfish) was also common to the entire area and was the fish most sought in the area by both sports and commercial fishermen. (Simmon & Breuer, 1962). While the Gulf surf is thought to be the spawning grounds of the mature redfish, no eggs or larval redfish have been taken either from the Gulf beach or from the passes, even though mature redfish were common in the bays near the passes in late fall and in the Gulf surf in winter. The bay nursery grounds of the juvenile redfish extend along the bay side of Padre Island from the Queen Isabella Causeway north for a distance of twelve miles. Redfish of less than one year (7 to 10 inches) were common in the Arroyo Colorado, Cayo Atascosa, and the Intracoastal Canal near Green Island during the summer months.Year class I to III were abundant throughout the year on the flats, principally along the bay shore of Padre Island. Some year class IV and older fish entered the bay in late fall and apparently engaged in heavy feeding before returning to the Gulf to spawn.

Ieiostomus xanthurus (Lacépède) the spot croaker is found throughout the area but not in large numbers. The ova and larvae are not known to the area, and specimens of over 8 inches are rare.

Micropogon undulatus (Linnaeus) The golden croaker was very common to the region. Juveniles appeared at the passes and in the Gulf surf in December and January. By February the entire bay was filled with 20 to 40 mm croaker. Specimens of five to eight inches were plentiful in the channels during the summer. Large schools of adult croaker have been reported in the Intracoastal Canal but have not been observed. A few 35 to 40 mm specimens have been taken near the passes in January and some with roe south of East Channel in October. Spawning apparently occurs in the Gulf during late fall (Pearson, 1929).

Menticirrhus littoralis (Holbrook). The whiting or "ground mullet" was common in the surf of Padre Island but seldom entered the bay area.

Pogonias cromis (Linnaeus). The black drum was very common throughout the bay area, especially from Three Islands north. (Simmons & Breuer, 1962) Juvenile drum have been found in the Arroyo Colorado, Cayo Atascosa, and in the shallow sloughs west of Port Isabel in the late spring and early summer months. Drum of from 7.5 to 22.5 mm known as "butterfly drum," were common in the Intracoastal Canal from Three Islands to Port Mansfield during the summer months. Adults were numerous on the flats throughout the year, often traveling in large schools. Severe cold weather caused them to move to the channels. Influx of fresh water caused them to migrate up the Arroyo Colorado and the floodways. Large drum were common in the surf during the winter months. Not usually sought by sports fishermen, these large drum are of marketable value to the commercial men.

The Game and Fish Commission, operating under authority of the Legislature, has been attempting to reduce an excessive black drum population in this area by authorizing contract drum netting in Cameron and Willacy counties during certain

winter months. This netting alone has resulted in the harvest of over 750,000 pounds in 1959–60 and over 1,000,000 pounds in 1960–61.

Abudefduf saxatilis (Linnaeus). The sergeant-major is a resident of the Brazos Santiago jetties.

Two specimens of parrot fish were taken at Station 15 during May and June 1956 but not yet identified.

Chaetodipterus faber (Broussonet). Spade fish of all sizes are common at the Brazos Santiago jetties.

Spheroides sp. Small specimens of a species yet undetermined are common at Port Isabel.

Chilomycterus schoepfi (Walbaum). The spiny boxfish is common from the Queen Isabella Causeway north to Three Islands during late spring and early summer.

Scorpaena sp. Common at Station 15.

Prionotus sp. A few sea robins were taken near the Queen Isabella Causeway but were not common.

Dormitator maculatus (Bloch). Two sleepers were taken in the Arroyo Colorado during periods of excessive fresh water.

Erotelis smaragdus (Cuvier and Valenciennes). The emerald goby has been taken at Station 15 but is not common.

Astroscopus y-graecum (Cuvier and Valenciennes). Two specimens were taken each at the mouth of the Arroyo and at Station 15, not common.

Opsanus beta (Goode and Bean). The oyster dog or toadfish was common over much of the area, especially at the mouth of the Arroyo and at Station 15.

Citharichthys spilopterus Gunther. The spot-finned whiff was common in the trawl samples in and adjacent to the Brazos Santiago channel.

Ancylopsetta quadrocellata Gill. The ocellated fluke was fairly common from the approach to the jetties to Port Isabel.

Paralichthys albiguttus Jordan & Gilbert. The Gulf fluke was a resident of the open Gulf, where it was taken in quantity by the Gulf shrimp trawls. A few specimens enter the bay and are common near Port Isabel.

Paralichthys lethostigma Jordan and Gilbert. The southern fluke is the commercial flounder of the area and was found throughout the entire area. Most common during the warmer months, some mature individuals remained in the area throughout the winter. Specimens from 35 to 50 mm were taken in December.

Symphrus plagiusa (Linnaeus). The tonguefish was fairly common in trawl drags adjacent to the approach to the Brazos Santiago channel. Young of 20 to 30 mm have been taken in January near Port Mansfield.

Histrio histrio (Linnaeus). The sargassum fish was common to the area near Port Isabel, where it was found among its usual habitat, the sargassum weed.

Ogcocephalus radiatus (Mitchill). Two specimens have been taken at Station 15, not common.

Fish Mortality

Abnormal mortalities of fish in the lower Laguna Madre were caused by pollution, sudden drops in water temperature, sudden influxes of fresh water, and by red tide.

Pollution was not a serious problem in the area. Some minor fish kills in municipal

or industrial areas have occurred (Port Brownsville and Port Harlingen) but little or no effect was noted in the Laguna Madre proper.

Sudden drops in water temperature during excessively cold and prolonged northers have done catastrophic damage to marine life in this area in the past and undoubtedly will in the future. The "freeze" of February 1951 caused great damage to fish, and this was reflected in sports and commercial landings for the next three years. No significant fish kills due to "freezes" occurred from 1951 to 1959.

During periods of heavy rains or river flooding, a sudden drop in salinity often killed fish in the Arroyo Colorado. Flounder, trout, catfish, hardhead catfish, blue crabs, and shad were the principal victims, but the total number was minor as compared with the total population of these species in the bay proper is such that the damage is negligible.

On and about September 10, 1955, a heavy concentration of *Gymnodinium brevis* in the Gulf surf caused a "red tide" kill on the island beach from the mouth of the Rio Grande to a point some 15 miles north of Brazos Santiago Pass. Samples taken by the U.S. Fish and Wildlife Service showed 50 to 500 individuals of *G. brevis* per ml of water. Kill was moderately light, and only scrap fish were affected. Sixteen days later, another kill was reported in the same area. Found dead were bull and rat reds, pike, trout, drum, and pompano, along with many scrap fish.

These two "red tide" kills coincided with earlier rains, increased flow of the Rio Grande, and warm temperatures. No red tide organisms were found in the bay samples. Kill in both cases was considered light.

Since the dredging of the Intracoastal Canal in 1948, fish kills due to hypersalinity have not occurred.

Effects of Dredging in South Bay

South Bay (Fig. 4), the southernmost bay area, lies between the Brownsville Ship Channel and the Rio Grande. Major ecological changes have taken place there in the past twenty-five years due to spoil from dredging. The Brownsville Ship Channel was completed to a depth of 28 feet in 1938, and much of the resulting spoil from the east end of the channel was placed in a line along the north end of South Bay. This and subsequent redredgings effectively closed the entrance to South Bay with the exception of a narrow, shallow inlet. This spoil deposition prevented the natural water circulation from the Gulf, through South Bay and Boca Chica Pass into the Laguna Madre. Boca Chica Pass was dependent on the strong annual northers to push large volumes of water from the Laguna Madre, through South Bay, and out through the pass to keep it scoured. As a result of the spoil deposition, Boca Chica Pass filled in rapidly and closed finally in 1945. Since that time, circulation in South Bay has become non-existent, and average water depth has decreased from 4 feet to an average of less than 18 inches, and each subsequent re-dredging of the channel reduces the average depth even more.

The layers of dead oyster shell correspond to the layers of deposited spoil and indicate that much of the South Bay oyster population was destroyed with each dredging operation. Commercial oystermen reported decreased harvest following dredging operations. Commercial and sports fishermen report fishing in South Bay has been reduced to insignificance. The pumping of mud into the bay was more rapid than the ability of the vegetation to cover it, resulting locally in water of very high turbidity. A series of bars

has been built up across the bay which retards circulation and prevents boat travel in the bay. The bay bottom is mostly of soft mud.

Port Mansfield Pass

Since the initial completion of the East Channel, pass, and jetties in October of 1957, several notable changes have occurred in the ecology of the adjacent bay area.

The crop of class O year redfish throughout the lower Laguna Madre in the summer of 1958 was notably greater than in many years past. This increase was noted in commercial landings at Port Mansfield, which showed a substantial increase in year class I plus during the summer and fall of 1959. There was another excellent crop of class O redfish in summer of 1959. These two consecutive yearly increases in young redfish production coincided with the first two years after the opening of Port Mansfield pass.

Prior to the opening of the pass, the summer juvenile brown shrimp populations of the Lower Laguna Madre seldom extended north farther than Station 21, as shown by monthly trawl samples made throughout the period. Since the opening of the pass, however, brown shrimp have been taken in quantity at all stations in Redfish Bay, and sizable concentrations were noted in April of 1959 in Redfish Bay along the Padre Island shore from East Pass to the land cut.

The landings of flounder by both sports and commercial fishermen have increased manyfold since the opening of the Pass. Increased commercial landings are reported by Port Isabel and Port Mansfield fish dealers, and increased sport catches were reported by bait stand operators and noted by personal observations. Flounder, which previously had seldom ventured north of the Cameron-Willacy County line, are now abundant north to the land cut.

Vegetation, both shoal and widgeon grass, has increased in the area, both in range and in stand. This was shown by comparing vegetative mappings by the author in 1955 and 1957 with mappings made by Mr. James Pipkin, Wildlife Biologist for the Texas Game and Fish Commission in 1961.

Pig fish, *Orthopristis chrysopterus*, the most preferred food of the sow trout, have appeared throughout the area in large amounts. Prior to the opening of the pass, the piggy was rare in the area and taken only as scattered individuals.

Prior to 1957, adult and juvenile pinperch, the most important bait fish of the area, entered the Laguna Madre through Brazos Santiago Pass in late January and early February and migrated steadily northward. It was late April and early May before this population reached the extreme north end of Redfish Bay as evidenced by extensive trawl sampling. Since 1957, pinperch populations return to the area as early as late January, providing food for the trout at least three months earlier than before.

In addition, the fall migration of pinperch to the Gulf was delayed at least a month so that a sizable pinperch population existed in Redfish Bay for 10 to 11 months (January to November) as compared to six to seven months (May to November) prior to the opening of the pass.

It has also been noted from trawl samples that juvenile trout have been located in abundance on the established grass beds which have increased in stand since the opening of the pass. This has occurred in areas where juvenile trout were not recorded prior to 1957.

Summary

1. Hydrographic data and annotated comments on species are presented for the lower Laguna Madre, an elongated lagoon seventy-four miles in length and three to eight miles in width in Cameron, Willacy, and Kenedy Counties of South Texas, separated from the Gulf of Mexico by Padre and Brazos Islands. Water depths range from twelve feet to a few inches, and the total water area is in excess of 150,000 acres.

2. This bay is noted for a high production of spotted trout, redfish, and black drum.

3. Fish kills are caused by pollution, "red tide" influxes of fresh water, and by extreme cold temperatures.

4. Planktonic species forms are most varied near the passes and during the summer months.

5. Brown algae are very common in Port Isabel Bay especially *Gracilaria blodgetti* Harvey.

6. Five species of spermatophytes are present in the area with *Diplanthera wrightii* Aschers most widely distributed.

7. The sponges and coelenterates are largely confined to the area adjacent to the Gulf.

8. Ctenophores are common throughout the area, especially in the winter months, with *Beroë ovata* Chamissa and Cypenhardt the most common species.

9. Annelids are present all over the area, inhabiting the oyster beds, and sand or mud bottom. Several forms are important to the diet of game fish.

10. Of the many species of copepods present, only *Acartia tonsa* Dana is abundant over the entire area. Most other species are abundant only near the passes.

11. Barnacles are present wherever there are places for attachment.

12. Amphipods are plentiful during the summer months among the algae and spermatophytes and contribute to the diet of many of the smaller fish.

13. Shrimp are common to the area with the juvenile form of the brown shrimp, *Penaeus aztecus* Ives, and *Palaemonetes intermedius* (Holthius) the most abundant.

14. Crabs are plentiful in variety and numbers. The male of the blue crab, *Callinectes sapidus* Rathbun is present in large numbers throughout the year. The young of this species is the most important item in the diet of the two to four year class redfish.

15. The commercial oyster population of *Crassostrea virginica* Gmelin present in the Port Isabel area is capable of spawning, setting, and rapid growth in a salinity range of 32 to 42 ‰. Other small bivalves contribute to the diet of the black drum of the area.

16. A variety of nudibranchs are common to the Port Isabel area, including several species not previously reported in Texas.

17. The fishes of most importance to the sport and commercial fishery of the area include the spotted trout, redfish, black drum, flounder, croaker, sheepshead, pike or snook, and tarpon. The more important bait fishes are the anchovies, silversides, mullet, pinperch, piggies, skipjack, killifishes, and gobies.

18. Normal salinity range over the entire area ranges from 32 to 35 ‰ near the passes to 50 to 55 ‰ at the extreme northern end of Redfish Bay.

19. Turbidity is greater in the shallow, barren, unprotected waters over mud bottom and less in the wind protected, vegetated areas over sand bottom.

20. The temperature of the shallow, wind exposed areas vary with the most extreme air temperature ranges.

21. Effects of tides are more noticeable at the passes and become less noticeable away from the passes.

22. Currents are more influenced by the tides near the passes but as the distance from the passes increases, the current influence by tide is reduced and the influence by the wind is increased.

23. In the summer, the prevailing south-east winds cause currents to enter Brazos Santiago Pass and travel northward in the bay, and out through the Port Mansfield Pass and the land cut. The prevailing winter current is reversed by the prevailing northerly winds.

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A Study of Redfish, *Sciaenops ocellata* Linnaeus and Black Drum, *Pogonias cromis* Linnaeus[1]

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Abstract

Data on redfish, *Sciaenops ocellata*, and the black drum, *Pogonias cromis*, are presented from 1949 to 1959. Redfish spawn in the Gulf of Mexico during fall and winter months but the exact site of this spawning is uncertain. Young fish move through passes into nursery grounds into the bays where they remain from six months to three or four years. Growth is rapid and standard lengths of 320, 530 and about 700 mm. are reached during the first three years. Spawning normally occurs at the end of the third or fourth year when the fish are 700–800 mm long, but ripe fish as small as 450 mm. have been found. Although the species is euryhaline, individuals are most often found at salinity of 20–40 ‰. Extreme temperatures of 3–33° degrees C. are tolerated but sudden drops in water temperature cause mortality. The food of redfish is primarily crabs, but shrimp and small fish are also consumed. More redfish are found in the bays during spring and fall months than in winter or summer, but some are present all year. Migrations are much less extensive than had been supposed and intrabay movement is relatively rare. Some schools of redfish are almost permanent residents of the Gulf while others rarely leave the bays during the first three or four years of life.

Black drum spawn in all of the bays and over any type bottom, as well as in the Gulf near passes. Most spawning takes place in February or March, but there is a prolonged or split season in May or June. Growth is less rapid than that of redfish and standard lengths of about 160, 310, and 415 mm are attained in the first, second, and third years. Tagging results indicate growth of 50 mm per year after the third year. Drum are euryhaline and have been found in salinities from 0–80 ‰. At this higher salinity many are blinded or in poor condition, and spawning does not occur. There is a definite temporary movement to fresh water creeks during flood periods. Most movement is random during feeding; food consists primarily of small mollusks although vegetation, small fish, polychaete worms and shrimp are also consumed. Their habit of grubbing for food is detrimental to spawning areas of trout and nursery areas of trout, redfish and shrimp.

Parasitic copepods, primarily of the genus *Caligus* are found on both redfish and drum but are lost when salinity rises above 45 ‰. Few isopods have been found on either species.

Redfish are sought by sport fishermen in the bays and in the Gulf. Drum are less actively sought although there is a substantial tourist fishery for this species. Creel census figures (Simmons, 1959–60) indicate that over one million pounds of redfish are harvested annually by sports fishermen. Commercial fishing is limited by law but about two million pounds of redfish and drum are harvested each year by various commercial means. Catastrophic freezes occurring about every ten years have each destroyed more fish than have been harvested commercially for the past 50 years.

Drum are considered to be detrimental to trout and redfish populations since they destroy spawning and nursery grounds, compete for food and space, and are less restricted in spawning requirements. The Laguna Madre tends to become overpopulated with this species very quickly. In an effort to reduce their effects, rough fish permits, for drum only, have been issued for certain parts of the Laguna Madre.

Introduction

The speckled trout, redfish, and black drum, all of the family Scianidae, are three of the most important sport and commercial fish of the Texas region. Guest and Gunter (1958) recently consolidated scattered data on the speckled trout and squeteagues of the genus *Cynoscion*. Using the format of their paper, information on the redfish, *Sciaenops ocellata* (Linnaeus) and the black drum, *Pognias cromis* (Linnaeus) is sum-

[1] Contribution No. 49 of the Texas Game and Fish Commission Marine Laboratory, Rockport, Texas.

marized in this contribution which includes data from recent surveys, unpublished reports, and scattered literature, especially by Pearson (1929), Gunter (1942, 1945, 1946, 1950, 1952), and Miles (1949, 1950, 1951). Areas sampled extended from Pass Cavallo to Port Isabel, Texas (Fig. 1). After separate sections are presented on description and life history of each species, the roles of both species in the sports and commercial fishery are discussed.

Redfish

Description

A full description of the redfish (*Sciaenops ocellata*) was given in Jordan and Evermann (1900). Color was reported as "grayish silver, iridescent, often washed with copper red; each scale with a center of dark points, these forming rather obscure, irregular, undulating brown stripes along the row of scales; a jet black ocellated spot about as large as eye at base of caudal above, this sometimes duplicated; the body occasionally covered with ocelli."

The authors have noted in this study as many as 219 ocelli on an individual fish. The color was normally silvery when the fish had been in Gulf water or in bays with sandy substrate. Those fish captured from turbid water were often coppery, dark, and sometimes almost black. Fish normally captured in Texas bays ranged in weight from one to thirty pounds, but large fish were known to exist in the Gulf of Mexico. Very large redfish had blunt heads, often with a lumpy appearance.

Distribution

Redfish range, on the Atlantic coast, as far north as Massachusetts and as far south as southern Florida. Joseph and Yerger (1952) reported that at Alligator Harbor, Florida, they collected redfish adults only in September and that six young were collected in March and five more in July. Henry Hildebrand in an oral communication stated that redfish were numberous at Tampico, probably present at Tuxpan, and had not been reported from Vera Cruz. This particular species was found most often in bays or lagoons or in the Gulf surf, but there was one report of a very large school of big redfish at a point 12 miles offshore from Sabine Pass, Texas in 1948 verified by the authors. There have been many unconfirmed reports and one confirmed occurrence from snapper banks near Port Isabel. Planes have sighted many large schools in the Gulf of Mexico.

Life History

Data concerning sexual maturity and spawning activity have been difficult to obtain as adult redfish normally are found only in inaccessible Gulf water during the spawning period. (Gunter, 1945). Most of the mature stock is derived from the Gulf although Pearson (1929), Miles (1950), Breuer (1957) and Simmons (1957) noted movement of small aggregations of adult fish from the bays to the Gulf.

Spawning takes place in late summer (Miles, 1951) and early fall (Pearson, 1929, and Gunter, 1945a, 1950). A few ripe fish were captured in the upper Laguna Madre on January 20, 1960. The presence of small redfish, 50–125 mm long, in the upper

FIG. 1. Map of the study showing movements of tagged redfish.

Laguna Madre in April 1953, 1954, 1955 and 1960 indicates that these fish were spawned in November, December and January.

Pearson (1929) noted that maturity is reached at the end of the fourth or fifth year and stated that no redfish under 750 mm were taken in a mature condition. However Gunter (1950) found ripe fish only 425 mm long, Miles (1950) found one gravid female 625 mm long and ripe males 500 mm long and ripe females 550 mm in length were caught in the upper Laguna Madre in January 1960.

The exact site of spawning is uncertain. Pearson (1929) observed adult redfish milling about the mouths of passes in October and November and one of the authors observed this activity in October 1950 near Cedar Bayou Pass. In each instance spent adults were found near the beach but no eggs were recovered. Cheesecloth pushnets used in the surf in 1953, 1954, and 1955 took large numbers of other sciaenids but few redfish, and intensive sampling by Hildebrand (personal communication) and by Simmons in 1959 and 1960 failed to obtain this species. Pearson (1929) has shown that the youngest redfish are found in the bays just inside passes with larger juveniles moving further into the bay. This indicates spawning takes place in the Gulf or the passes.

Mansueti (1961) postulated that planktonic *Sciaenops* are carried into Chesapeake Bay in September by deep subsurface water currents of high density.

Description, Early Development, and Habits of Young. Pearson (1929) described young redfish four or five millimeters long as follows:

> "The yolk sac is present and the dorsal and ventral fin folds are continuous to the caudal fin. The latter is fairly well developed, as are the ventral fins, although the rays of both dorsal and anal are indistinct. Ventrals and pectorals are obscure. One or several prominent groups of brown chromatophores or pigment areas are present invariably and these serve, by their approximate location to help identify the young fish at this early stage."

During the more recent part of this survey no fish of such small size were located. However, sciaenids 12–15 mm long, captured in the surf, all appeared to have identical markings and body shape. These, when allowed to grow in aquaria, proved to be mostly golden croaker with only an occasional redfish. A more reliable means of identification is afforded by the relative shape of the caudal and pectoral fins. The pectoral fin of the redfish is more pointed than that of the croaker but the caudal fin is less pointed in the redfish than in the croaker.

By the time the fish are 25 mm long, barbels are present on croakers and pigmentation is distinct on redfish. There are 20–50 dark, distinct blotches from the lateral line to the dorsal fin on each side of the trunk and those along the lateral line are somewhat enlarged. At a length of 42 mm the juvenile redfish is morphologically identical to the adult except for the slightly more pointed caudal fin and the lack of distinct ocelli. (Fig. 2). These distinguishing spots are faintly visible at 50 mm and very apparent at 75 mm.

Very young redfish are found in protected water with little wave action. There is a distinct avoidance of currents and a preference for isolated grassy clumps or slightly muddy bottom. Young redfish first appeared in primary bays in August (Miles, 1950) but have not been found in the Laguna Madre, a secondary bay, before February. By April, widely scattered aggregations can be found in sheltered grassy areas throughout

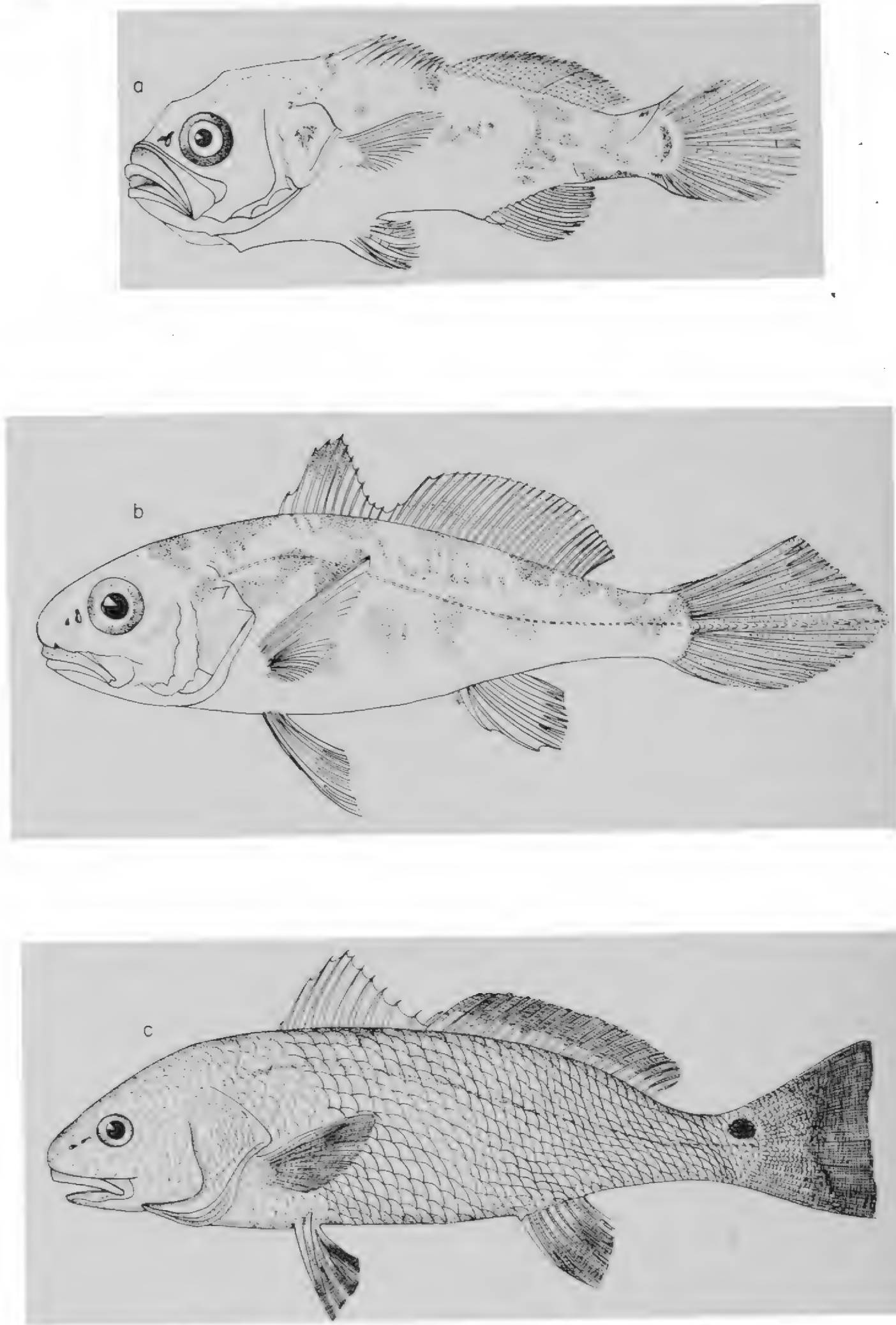

FIG. 2. Larval and juvenile redfish, modified after Pearson, 1929.

the Laguna Madre. In early April 1954, many redfish, 100–150 mm long, were captured in boat basins in the Laguna Madre. Subsequent seining revealed that large schools were present in every boat basin, in quiet areas near spoil banks, and in shallow

isolated sloughs. This occurred in years when salinity was between 40 and 50 ‰ but during years of lower salinity the fish were scattered over grassy flats as noted by Pearson (1929), Gunter (1945, 1950), and Miles (1950). The large schools remained in basins until late May when they began to scatter, and by June no sizable concentrations could be found. This coincided with the movement of small redfish through passes to the Gulf as described by Simmons and Hoese (1959). Returns of tagged fish indicated that many of these small redfish did move toward passes while others moved into primary and secondary bays.

Growth. Redfish grow more rapidly than trout or drum. Pearson's (1929) smoothed length frequencies are marked by modal lengths of 300, 530, and 630 mm at the end of the first three years. Gunter (1945) gives the values 400 mm and 600 mm for the first two years while Miles (1950) indicates modal lengths of 320 and 510 mm for these year classes. This later growth rate is substantiated by returns from tagged fish in which the average growth per month was calculated and then prorated for one year (Table 1).

TABLE 1

Growth of redfish between the end of the first year and the end of second year as calculated from tag returns.

	Total length at one year mm	Total length at two years mm	Growth, second year mm
	325	528	203
	325	548	223
	325	426	101
	325	477	152
	325	629	304
	325	554	229
	325	565	240
	325	452	127
	325	680	355
Mean	325	540	215

Growth, however, is not constant. Length frequencies of 2,000 redfish of year class 0 from the upper Laguna Madre (Fig. 3) show sporadic growth with a lag in spring, rapid growth in summer, and a slight lag at the end of summer. The large size range during this first year may be due to the long spawning season but there is also some variation in the growth of individual fish as evidenced by tag returns. Fig. 4 shows graphically the size of fish when they were tagged, the time freed, and the size at the time of recapture. Table 2, showing the growth of redfish over two years old, indicates a length of 640–730 mm at the end of the third year with a mode of about 730 mm. This result suggest that Pearson's (1929) year class IV was year class III and that maturity is reached at the end of the third year.

Little is known of growth after three years of age. Miles (1951) examined otoliths of a small number of redfish 825–1,000 mm long and noted that those 875 mm long showed six rings while those 925 mm long showed seven rings. Pearson (1929) found small modes at 750 mm and 840 mm and felt that these probably represented year classes IV and V. One tagged redfish, recovered at a probable age of three and one-half years, was 810 mm long.

One interesting aspect of growth occurred at Eighth Pass, Mexico where Miles (un-

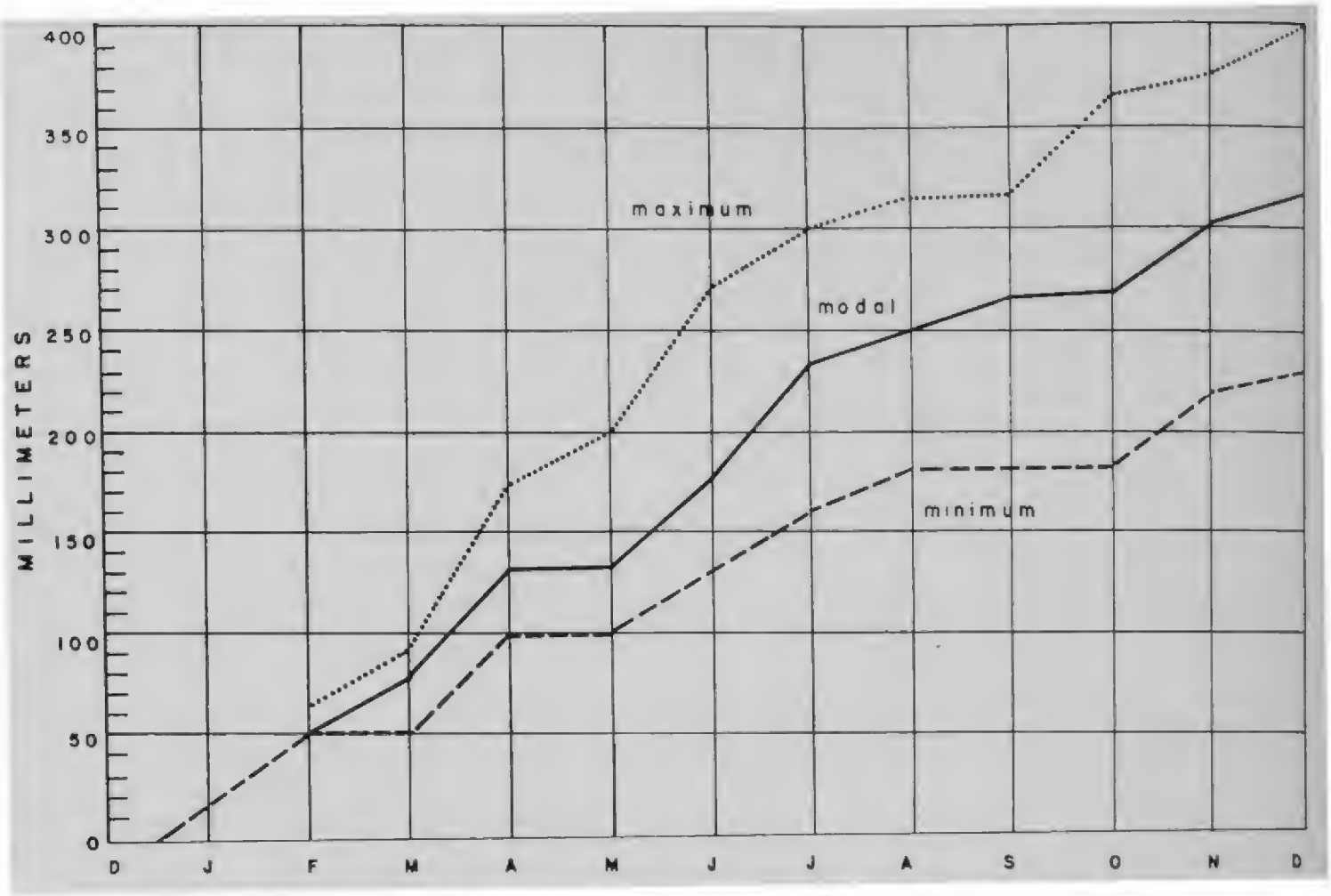

FIG. 3. Maximum, modal, and minimum lengths of 2000 redfish of year class zero.

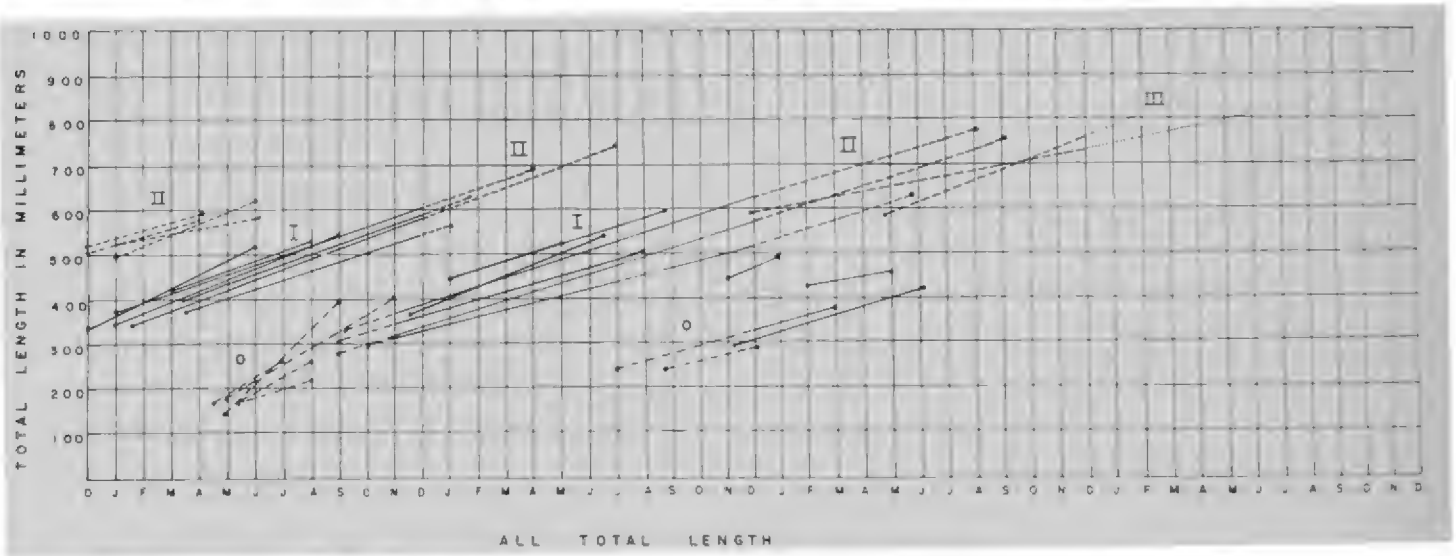

FIG. 4. Actual growth of tagged redfish by year classes.

TABLE 2

Growth of redfish between end of second year and end of third year.

	Total length at two years mm	Total length at three years mm	Growth, third year mm
	530	705	175
	530	678	148
	530	715	185
	530	730	200
	585	675	90
	585	845	260
	585	845	260
	585	765	180
	585	755	170
	585	885	300
Mean	563	760	197

published data) found that redfish of year class O were only 200 mm long in late July. This was 50–60 mm less than comparable fish in the Upper Laguna Madre.

Food. Very young redfish subsist primarily on copepods, amphipods and palaemonetid shrimp. At a size of 100–175 mm the chief food items are small penaeid shrimp, palaemonetid shrimp, small mullet and silversides, small gobies and small crabs. Pearson (1929) covered the area from Matagorda Bay to Baffin Bay and reported shrimp as the chief item in the diet of redfish. Gunter (1945) found that "the blue crab exceeded any other species in number of times found in the stomach and in volume it was far greater than any other food. It is the principal food of the redfish." He also found grass and wads of amphipods. Knapp (1948) who was primarily concerned with the incidence of menhaden in the diet, examined stomachs of fish brought in by charter boat operators at Port Aransas and compiled the data of Wilson, Robinson and Bowers (unpublished reports of the Texas Game and Fish Commission). These data show that over 68 per cent of those redfish with food in the stomach had eaten crabs. Miles (1948–49) examined stomachs of redfish caught in nets thus avoiding contamination of data by bait shrimp from sportsfish catch. He found that crabs, shrimp and small fish were major components of the redfish diet (Table 3). In the Laguna Madre the primary source of food is small crabs. The mud crab, *Neopanope texana*, and the immature blue crab, *Callinectes sapidus* Rathbun constitute most of the small crab population of the area and both are utilized to a great extent. Small shrimp, *Penaeus aztecus* Ives, prawns, *Palaemonetes intermedius* (Holthuis) and sheepshead minnows, *Cyprinodon variegatus* Lacépède are utilized to a lesser degree. Oddly enough, redfish do not take crabs used as bait unless the crab is halved and its legs removed.

Feeding Habits. Feeding usually takes place in the early morning and late evening often in shallow waters influenced by tides. In some cases the water is so shallow that the backs of the fish are visible.

Movements and Migrations. Pearson (1929), Gunter (1945a), and Miles (1950) have described a general migration of redfish to the Gulf during fall months and a fairly rapid return to the bays in spring. These movements do occur but may be less pronounced and cover shorter periods than had been assumed. Records of redfish landings by sportsfishermen, by commercial means and by biological nets (Fig. 5) indicate that more redfish are present in the bays in spring and fall than in either summer or winter but many are present at all seasons.

There was no pronounced migration of redfish through Cedar Bayou Pass in 1950–51 according to the records of a two-way fish trap attended by one of the authors and described by Simmons and Hoese (1959). Small redfish moved in and out of this pass in June and there was a slightly accelerated outward movement in September and October and during sudden drops in temperature. No mature redfish were ever observed moving through the pass although some were seen near the Gulf entrance in April and September. Since bay populations do fluctuate it is possible that larger, deeper passes were used.

Movement of tagged fish (Fig. 1) show that this movement is random within a bay and that there is little intra-bay movement or bay-gulf travel except perhaps for short periods. Similarly these tagging results show that redfish tagged in the Gulf remained in the Gulf for at least two years and probably permanently. It is possible that any tagged fish will leave an area and then return but Table 4 shows that the per cent

TABLE 3

Food of 1197 redfish, *Sciaenops ocellatus*, taken at or near Rockport, Texas, from September, 1948, to June, 1949 (after Miles, 1949, 1950)

Food item	Number	Per cent of incidence
Unidentified shrimp	1207	40.0
Shrimp, *Palaemonetes spp*	136	6.1
Shrimp, *Crangon spp*	54	1.8
Shrimp, *Penaeus spp*	11	0.3
Shrimp, *Penaeus aztecus*	29	0.9
Shrimp, *Penaeus duorarum*	5	0.16
Unidentified crabs	455	15.0
Blue crab, *Callinectes sapidus*	50	1.6
Gulf crab, *Callinectes danae*	21	0.6
Crab, *Callinectes spp*	20	0.6
Stone crab, *Menippe mercenaria*	9	0.3
Spider crab, *Libinia dubia*	1	0.03
Mud crab, *Eupagurus spp*	1	0.03
Unidentified fish	496	16.0
Silversides, *Menidia beryllina peninsula*	148	4.9
Mojarra, *Eucionstomus gula*	138	4.6
Flatfish, *Paralichthys spp*	18	0.6
Anchovy, *Anchoiella epsetus*	14	0.4
Unidentified eels	14	0.4
Pigfish, *Orthopristis chrysopterus*	13	0.4
Menhaden, *Brevoortia spp*	7	0.23
Mollies, *Molliensia spp*	5	0.16
Pinfish, *Lagodon rhomboides*	3	0.10
Pipefish, *Syngnathus spp*	3	0.10
Catfish, *Galeichthys felis*	3	0.10
Killifish, *Fundulus similis*	2	0.06
Croaker, *Micropogon undulatus*	1	0.03
Blenny, Family Blennidae	1	0.03
Lizard fish, *Synodus foetens*	1	0.03
Sea Horse, *Hippocampus spp*	1	0.03
Oyster shell, *Ostrea virginica*	12	0.4
Squid, *Loligo spp*	5	0.17
Annelid, *Nerina agilis*	12	0.4
Unidentified vegetation	9	0.29
Isopod, *Lavonica spp*	7	0.23
Uuidentified snail	2	0.06
Unidentified annelid	2	0.06
Algae	2	0.06
Gastropod	1	0.03
Turtle grass, *Thallassia testidinium*	1	0.03
Cricket	1	0.03

recaptured outside the area of tagging is small. It would appear that each bay, when considered on an annual basis, is a closed system.

Some general movements have been noted during the period from 1952 to the present. Redfish normally move before a strong wind, i.e., move in the direction the wind is blowing, but, when startled, move into the wind or current. There is either little movement during the day or little feeding as evidenced by the fact that few are caught in nets or on trotlines during daylight hours. Large schools are found in the Gulf.

Distribution in Relation to Salinity and Temperature. Redfish are euryhaline and have been found in fresh water (Gunter, 1942, 1956) and in salinities as high as 15 ‰ (Simmons, 1957). However, in the Upper Laguna Madre populations were rarely found at salinity of 50 ‰ or above and were most abundant at salinities of 30–35 ‰. One of the investigators (E.G.S.) has transferred small redfish directly from salt water

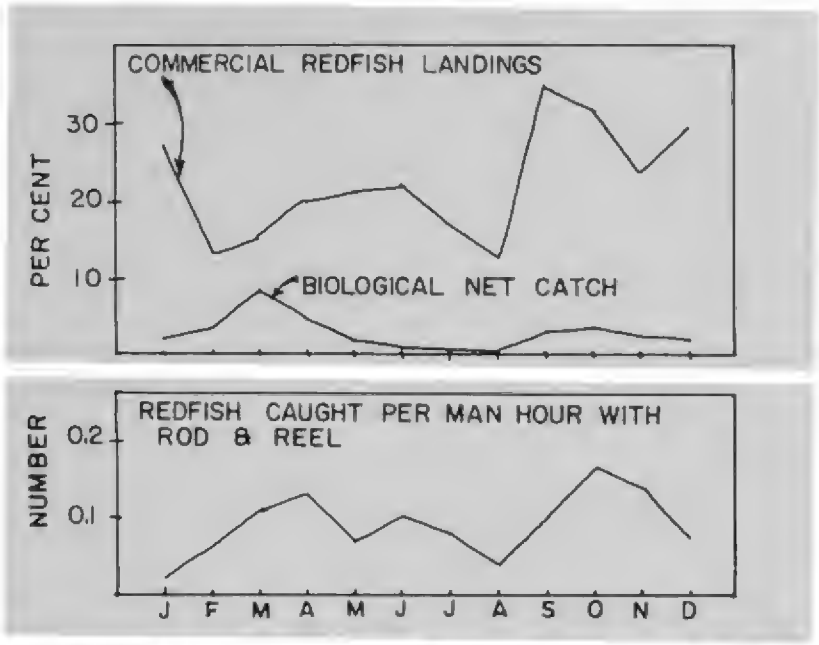

FIG. 5. Catch of redfish by various means, showing relative seasonal abundances.

TABLE 4

Recoveries of tagged redfish by year, class, and by area captured

Area	Year Class	Per cent recovered: Within bay where tagged	Per cent recovered: Outside bay	
Cedar Bayou	0	63.6	36.4	27.3% in Gulf 9.1% in Bay
	I	9.1	90.9	All in Gulf
Aransas Bay	All	57.1	32.9	16.4% in Gulf 16.5% in other bays
Upper Laguna Madre	0	90.2	9.8	2.0% in Gulf 7.8% in other bays
	I	95.0	5.0	All in Gulf
	II	100.0	0.0	.....
Lower Laguna Madre	All	86.0	14.0	All in Gulf

into fresh water ponds and eight individuals 600 mm long were captured two years later. Transplants, apparently successful, have been made into the Pecos River and into Lake Kemp but it is not known if these fish will spawn under such conditions.

Redfish have been observed by the authors in waters ranging from 2–33°C but normally they move into deeper water when extreme temperatures occur. Mass mortality sometimes occurs if there is a sudden change in temperature. Such "freezes" have been documented by Gunter (1941) and Gunter and Hildebrand (1951).

Black Drum

DESCRIPTION

A full description of the black drum, *Pogonias cromis* (Linnaeus), was given in Jordan and Everman (1900). Coloration was reported as "grayish silvery, with 4 or 5 broad dark vertical bars, these disappearing with age, usually with no oblique dark streaks along rows of scales above; fins blackish."

In this study the authors found that the coloration of black drum varies with the age of the fish as well as with its habitat. The typical adult was dark gray with a white belly. The characteristic four or five dark vertical bars of younger fish often disappeared with

age as noted above. Drum residing in the Gulf took on an almost uniform silvery appearance and lost the vertical bars at an early age while those residing in bays tended to become darker than their Gulf counterparts and are often bronze along the back and dirty white on the sides and belly. Breuer captured many drum in the turbid water of Baffin Bay. These were normally nearly jet black on the sides and back and had a gray belly. It was noted in Baffin Bay that many of the jet black drum were malformed, either by loss of eyes, mechanical damage to mouth or with deformed backbones. In contrast malformed drum in the Upper Laguna Madre did not exhibit the jet black appearance but possessed normal coloration. It is possible that many of the malformed drum in the Upper Laguna Madre received injuries from boat props. The senior author has observed commercial fishermen run motorboats through schools of drum feeding in shallow water, then go back and pick up a tubful of injured fish.

Dr. William McFarland reports (verbal communication) that severance of certain nerves in the head of some sciaenids brought about an enlargement of the chromatophores in the general area of the nerve severance. The high incidence of malformed jet black drum in Baffin Bay could be due to the inability of injured fish to follow usual migrations, and are thus restricted to this turbid area.

Distribution

Black drum occur along the Atlantic coast and Gulf coast from New York to the Rio Grande River and have been reported straying as far north as Massachusetts. Hildebrand (personal communication) reported finding none at Vera Cruz. Black drum are found in the bays even more than redfish; nevertheless a sizable population exists in the Gulf of Mexico. By far the heaviest concentrations are usually found in Corpus Christi Bay and in the Laguna Madre. Joseph and Yerger (1952) noted black drum rare at Alligator Habor, Florida, especially in summer. Frisbie (1961) indicated that young drum were relatively uncommon in the Chesapeake and Delaware Bay regions and that these young were normally found in fresh to brackish waters.

Life History

Black drum reach sexual maturity at the end of the second year when approximately 320 mm long. Spawning occurs in or near passes, in the Gulf, and in all bay areas. Miles (1950, 1951) reported that mature drum remained in bays until nearly ripe before migrating toward passes and, after spawning, quickly returned to their preferred bay habitat.

Sciaenid eggs, believed to be those of black drum, were found on March 20, 1952 near the Point of Rocks, and on the same date ripe drum were found in Baffin Bay. Other eggs were found throughout the upper Laguna Madre. Some of the ripe drum tagged near Baffin Bay remained in that location throughout the spawning season. Others moved into Corpus Christi Bay. In April 1960, eggs were stripped from a 40 pound drum and used for comparison with eggs taken in plankton tows. Developing eggs (Fig. 6) were found to be present in bay areas from February through April. Ripe fish have been found as early as December (all males) and as late as June, but 90 per cent of the known spawning occurs in February and March. However, length frequencies

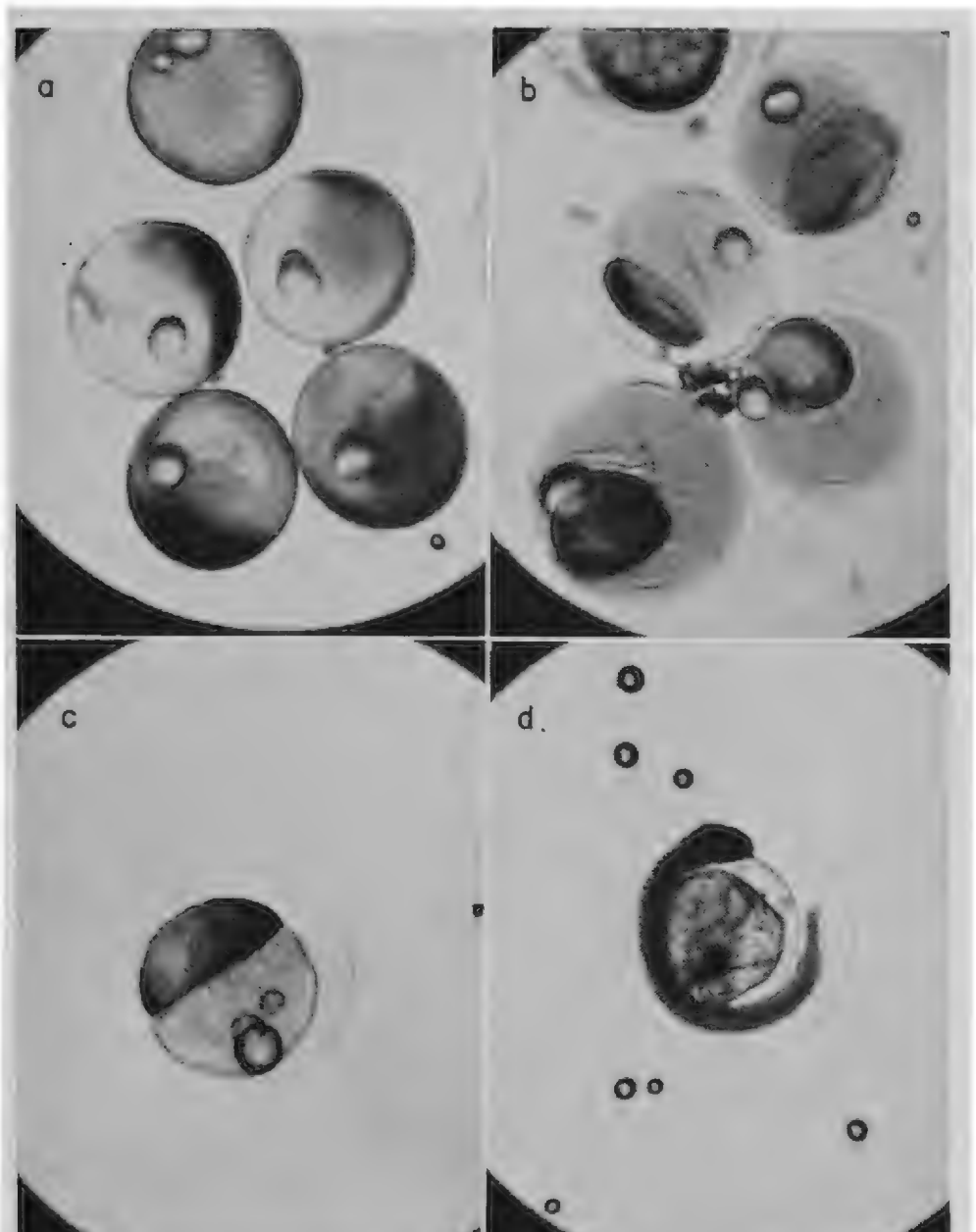

FIG. 6. a. Unfertilized eggs taken from ripe drum, April 12, 1960. b,c,d. Eggs taken in plankton tows, February-April, 1960.

(Fig. 7) indicate that there may be a split or very late spawning in June or July. This was also suggested by Pearson (1929).

Descriptions and Habits of Young, Early Development. Pearson (1929) gives the following description of young drum.

> "The larval drum begins to take on the general appearance of a drum when it reaches a length of about eight millimeters. Black chromatophores appear

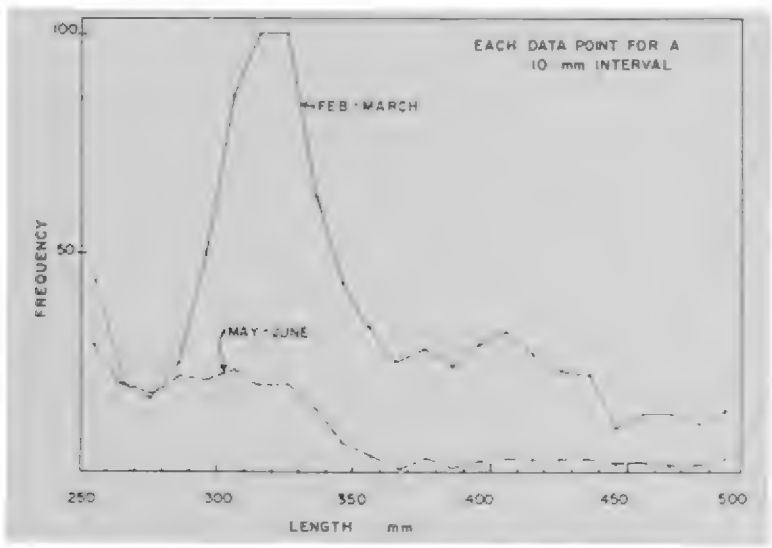

FIG. 7. Length frequencies of black drum caught in nets in the upper Laguna Madre.

> in great abundance along the back and sides of the fish and tend to arrange themselves into definite groups. These groups then arrange themselves into the six vertical bars which will serve to identify the immature black drum. The general adult shape is attained when the fish reaches 15 millimeters—.The black bars are well defined, the fins generally colorless, and the barbels on the lower jaw in evidence. At a length of 25 millimeters, the pectorals and anal fins take on a dark cast, the entire fish gradually becoming darker."

Pearson first located the larval drum of 9 to 37 mm (Fig. 8) along the shores of Corpus Christi Bay near the channel entrance to Oso Bay on May 13, 1926. He noted, however, that still smaller fish were found near passes to the Gulf. Many schools of small drum, approximately 50 mm long, were noted in the Laguna Madre at the entrance to Baffin Bay in June and July 1951, and even smaller drum, only 13–18 mm long, were found in the Upper Laguna Madre in May and June. These smaller drum were invariably located in channels, stagnant sloughs or boat basins. Many young drum, 130–180 mm long, were located in the Upper Laguna Madre in May and the same size fish were found in Baffin Bay and the Lower Laguna Madre from September through December. It appears that spawning and nursery grounds can be the same. Drum tend to enter a preferred habitat and to remain there. This type habitat, represented by all of the Laguna Madre and Baffin Bay and much of the shallow water of Corpus Christi, Nueces and Oso Bay, is utilized by the 0 year class as well as all other year classes including the largest sizes.

Growth. Considerable confusion exists concerning the growth rates of black drum. Pearson (1929) considered that fish just entering the second year had reached a fork length of 250 mm but stated that catches of fish 150 mm long in December were difficult to interpret and might be due to a late spawning or possibly a split spawning. This same situation was found to exist during later surveys. Drum only 13–18 mm long were found in late May and June when fish from the winter spawning were 50–75 mm. long. At the same time definite modes (Fig. 7) were found at 175 mm and 240 mm. In February and March these same modes were found, though less pronounced. If 175 mm fish were the result of a split spawning in summer, they would represent one year old fish; if they were the result of a late spawning they would be slightly over one year old. It seems probable that late or split spawning does occur, and that a standard length of 140–180 mm is reached in one year 210–250 mm in one and one-half years, and 290–330 mm. in two years. Although peaks are masked by overlapping there is evidence (Fig. 7) that drum reach a length of 400–430 mm in three years. Beyond that, tag returns, (Fig. 9) indicate a growth of about 50 mm per year.

Food and Feeding. The food of very young drum consists chiefly of marine annelids, small fishes and soft crustaceans. Larger drum feed on molluscs and shrimp. Pearson (1929) reported that the adult black drum's food was primarily mollusks and crabs while Miles (1949) showed that drum in Aransas Bay feed heavily on shrimp, mollusks, vegetation and crabs and only slightly on fish. (Table 5). In the Upper Laguna Madre and Baffin Bay all drum examined (about 1,000) had been feeding on small mollusks, and much dead shell had been consumed. Near Baffin Bay drum were found to be feeding on dead shell to which *Acetabularia crenulata* Lamarck and other algae were attached. Another food item was the sheepshead minnow, *Cyprinodon variegatus* Lacépède, which was taken in very shallow water. In a few instances polychaetes were found packed

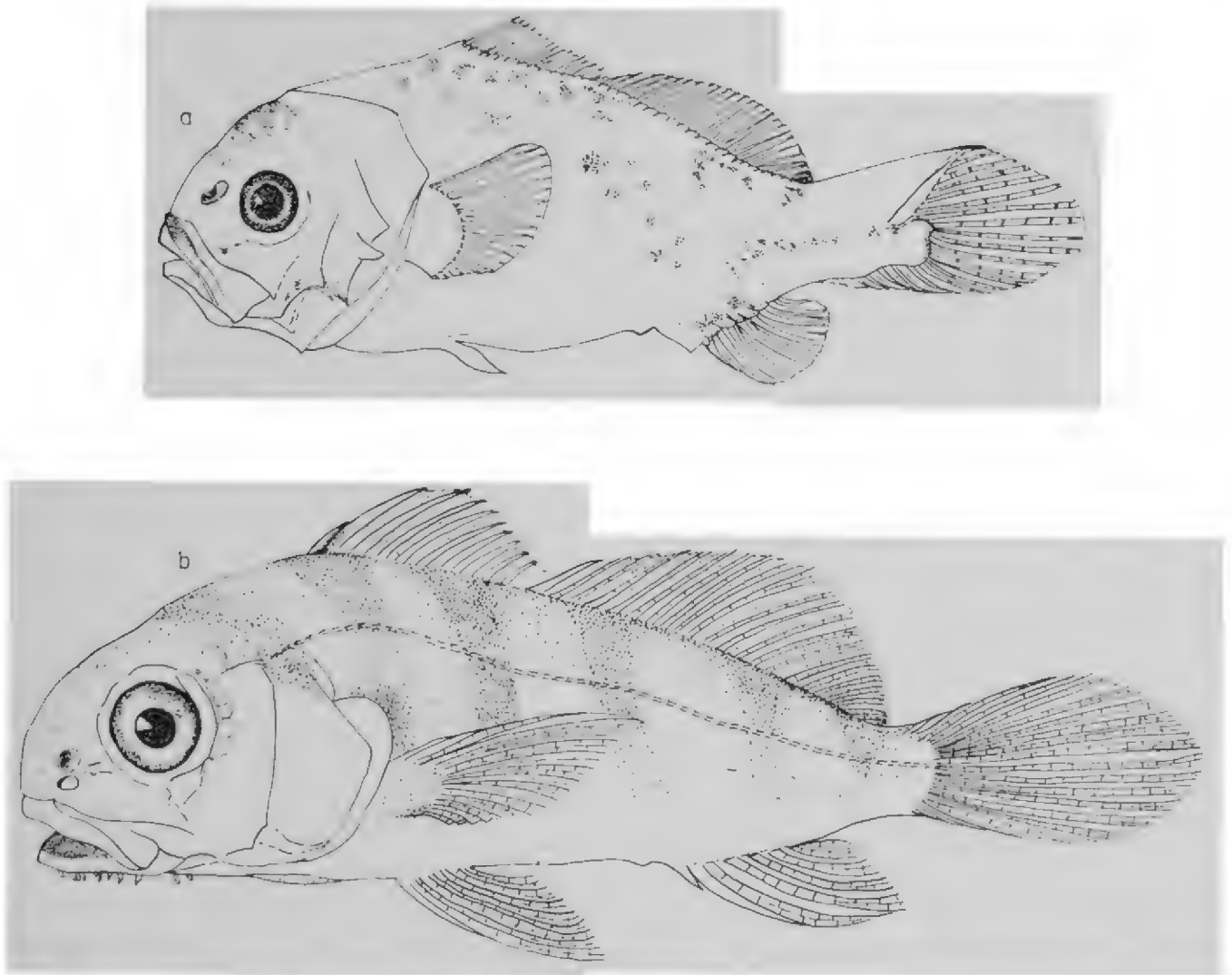

FIG. 8. Juvenile and adult black drum modified after Pearson (1929).

in the stomachs of fish examined and this coincided with lunar swarming of these small worms. In the lower Laguna Madre, salinity is less extreme and more species of mollusks are present. Species consumed include *Brachiodontes exustus* Linnaeus, small *Aquipecten irradians amplicostata* Dall, *Laevicardium mortoni* Conrad, *Anomolocardia cuneimeris* Conrad, and *Mulinia lateralis* Say (Fig. 10). While drum were observed feeding on or near oyster reefs, stomachs taken from these drum contained no oysters but rather a small mollusk, *Brachiodontes exustus*.

Most of the drum's food is taken from the bottom or from below the bottom. Mollusks

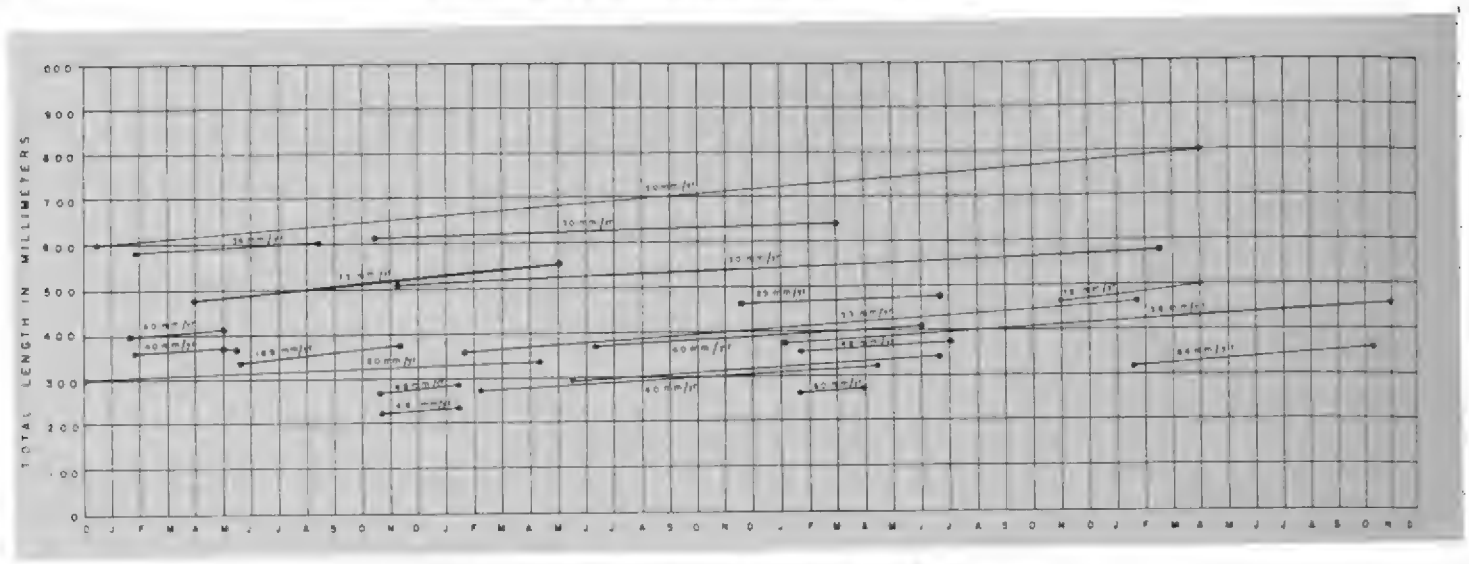

FIG. 9. Growth of tagged black drum.

TABLE 5

Food of 189 Drum, *Pogonias cromis*, taken at or near Rockport, Texas from September, 1948 to June, 1949 (after Miles, 1949, 1950)

Food item	Number
Shrimp, *Penaeus aztecus*	3
Shrimp, peneid type	2
Crab, *Callinectes sp.*	2
Crab, *Callinectes sapidus*	3
Pin Perch, *L. rhomboides*	1
Cyprinodon sp.	1
Venus clam, *Venus mercenaria*	5
Razor clam, *Tagelus gibbus*	7
Oysters shell	3
Venus sp.	5
Mulinia sp.	4
Bulla sp.	2
Donax variabilis	1
Annelids	1
Grasses	1
Algae, unidentified	1
Unidentifiable mass* (no. of stomachs)	49

* 55 shrimps, 12 crabs, 9 fish, and 20 mollusks constituted the unidentifiable organisms.

are grubbed from mud or sand and crushed with strong pharyngeal teeth (Fig. 11). Crabs were treated in the same manner but sheepshead minnows were swallowed intact.

Since mollusks are one of the favored foods of drum and since this food is often found under beds of vegetation, the normal feeding habits of drum are considered detrimental to these "grass" beds and consequently to sea trout, small redfish, and juvenile shrimp which use these areas as spawning or nursery grounds.

Movements and Migrations. Black drum are commonly found in hypersaline waters but can adapt quickly to wide ranges in salinity. A tendency for drum to move into streams inlets has been described by Breuer (1957). With the possible exception of spawning migrations this temporary surge to fresh water is the most pronounced and positive of all drum movements. There is also a constant movement in search of food and the fish often travel in large schools during these periods. When food is abundant there is little intra-bay movement. Of the 94 recovered tagged fish from the Laguna Madre and Baffin Bay (Fig. 12), 56 fish or nearly 60 per cent, were recaptured within five miles of the site of tagging. It must be noted that some of these fish were free for over

FIG. 10. Items commonly used as food by black drum. Left to right, top row: *Chione cancellata, Lithophaga paprecea, Aquipecten irradians amplicostatus, Brachiodontes exustus;* Bottom row: *Laevicardium mortoni, Anomalocardia cuneimeris, Mulinia lateralis.*

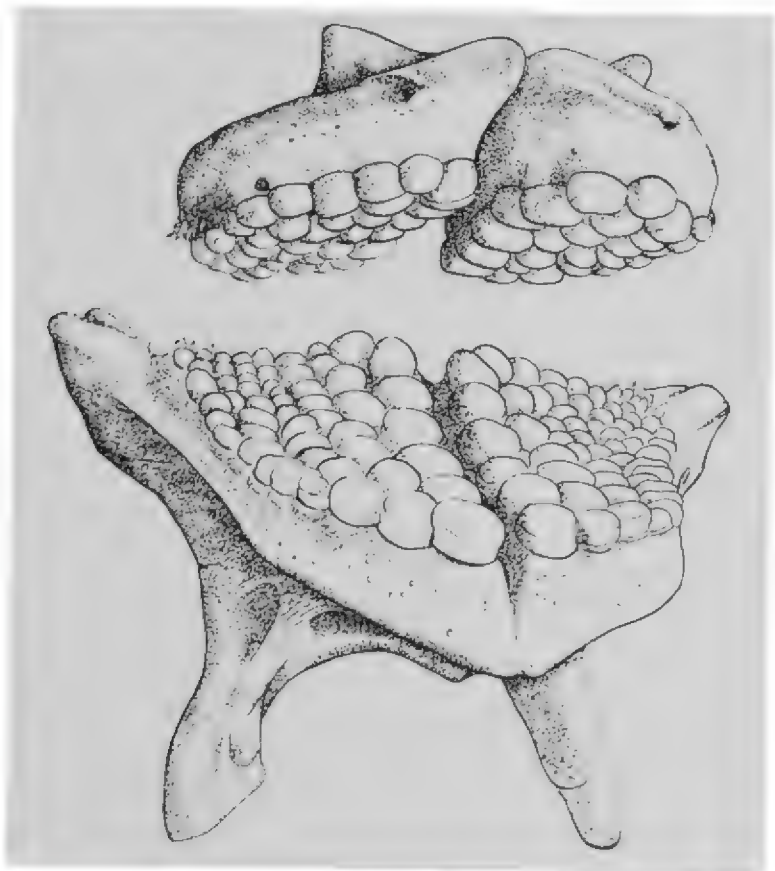

FIG. 11. Pharyngeal teeth of black drum, upper and lower.

two years and may have migrated greater distances. Eight fish moved southward into the Lower Laguna Madre and eight more were recaptured in Corpus Christi Bay. The movements northward are attributable to spawning but the cause for the southward movement is not known.

Movement may be accelerated by adverse conditions. In 1952 most tagged fish were recovered in the Laguna Madre. In 1953 hypersalinity and high temperatures destroyed most bivalves in the Upper Laguna Madre and a mass exodus of drum occurred. Tag returns indicate that these fish moved as far north as San Antonio Bay and returned to the Laguna Madre when food again became available. The longest migration recorded to date was from the central Laguna Madre to Texas City near Galveston, a distance of 245 miles covered in one year or less.

Breuer has noted that in the Lower Laguna Madre small drum are present all year and these move northward as spring approaches. At the same time large drum enter the bay at Brazos Santiago Pass and move northward. Shortly after this large schools appear in the lower section of the Upper Laguna Madre although too few fish have been tagged in the lower lagoon to verify the origin of these schools. There has been movement of at least 10 tagged fish southward from the Upper Laguna Madre into the Lower Laguna Madre during fall and winter months. These seasonal movements are complicated by the fact that there was a northward movement of tagged drum out of the Upper Laguna Madre during spring months (Fig. 12).

Very large drum are present in the entire Laguna Madre all year but are less abundant during summer months, at least in the Upper Laguna Madre. This is illustrated by creel census data (Simmons, 1959–60) which recorded an average weight of 15.0 pounds for drum caught in February and March compared to 2.0 for those caught in June or July, 1959.

Distribution in Relation to Salinity and Temperature. Black drum are euryhaline and frequently inhabit brackish or even fresh water (Gunter, 1956). Adults were found in August, 1953 at salinities as high as 80‰ although many fish had glazed eyes and some even were blinded and had lesions on the body.

Wide ranges in temperature are also tolerated, and schools have been found by the senior author apparently thriving, in turbid water only four inches deep where the temperature was 35°C. A sudden drop in water temperature causes movement to deeper water as in 1958 when drum from the upper Laguna Madre moved into Baffin Bay and Corpus Christi Bay. Water temperature at that time was 3°C and some of the fish were stunned but still capable of swimming. However, mass mortality is not uncommon when water temperature drops quickly and conditions remain adverse for long periods. Unpublished data of the Texas Game and Fish Commission indicates that during a five day "freeze" in 1951 more drum were killed than trout and redfish combined. The rapidity of recovery of drum populations is evidenced by the fact that gill net sets in October, 1951 caught only four drum while similar sets in the summer and fall seasons of 1952 caught between 138 and 426 drum per month (Simmons, 1952). It is further shown by U.S. Fish and Wildlife Service reports which list a decline in drum landings for the State of Texas from 708,300 pounds in 1950 to 702,200 pounds in 1951, while redfish landings dropped from 567,200 pounds to 237,000 pounds. Drum landings dropped only one per cent while redfish landings dropped 58 per cent.

FIG. 12. Movements of tagged black drum.

Parasites

Ectoparasites are fairly common on both redfish and drum of all sizes. They are normally absent when the fish is in hypersaline water above 45 ‰ (Simmons, 1957). Among these parasites are the copepods *Caligus repax* Milne Edwards, *C. bonito* Wilson, *C. latifrons* Wilson and *Brachiella gulosa* Wilson, all from the upper Laguna Madre. Causey (1955) also lists *Caligus pelamydis* Kroyer and *Brachiella macrura* Wilson from drum and *Echetus typicus* Kroyer and *Lernanthropus paenulatus* Wilson from redfish in the vicinity of Port Aransas. The only isopod found on sciaenids during this study in the Laguna Madre was *Nerocila acuminata* Schioedte and Neinert.

The most important internal parasite found in these fishes is the "Spaghetti worm" which appears to be similar to *Poecilancistrium robustum* Chandler, a pleurocercoid described from the muscle mass of *Cynoscion nebulosus* in Galveston Bay by Chandler (1935). These worms from trout are discussed by Parker (1951) and by Guest and Gunter (1958) They occur in the muscle mass of both redfish and drum and are more noticeable in large drum. The appearance of this worm in drum is the cause of objection by the public to its use as a food fish. However, the smaller fish are relatively free from this parasite—which is not harmful to humans in any state. (Parker, 1951) Sogandares-Bernal and Hutton (1959) reported helminth parasites from other members of this family and it is probable that some of these also occur in drum and redfish.

Sport Fishery

Sports fishing in Texas waters has increased tremendously in recent years with the advent of larger boats and motors. Bait stands have reported a three-fold increase in the number of boats rented and launched. A survey made by Belden Associates (1959) indicates sport fishermen caught 9,199,000 pounds of redfish and 4,343,000 pounds of drum from September 1, 1957 to August 31, 1958.

Creel census data from the upper Laguna Madre indicates a much smaller catch. During the period from August 1, 1959 to July 31, 1960 a total of 82,992 fishermen caught 39,536 redfish weighing 78,058 pounds in this bay which has a water area of about 100 square miles. At the same time 18,298 drum weighing 37,030 pounds were caught. If these values are expanded to cover the entire year and the entire State the catch would be about 975,000 pounds of redfish and 540,000 pounds of drum. Virtually all of the redfish captured were less than three years old and many were less than one year. Drum were caught in all sizes and ages. This species is not actively sought and less than 10 per cent of Laguna Madre fishermen fished exclusively for drum although many incidental catches were noted.

Tagging results (Table 6) indicate a heavy fishing pressure for redfish and, percentagewise, a larger portion of the population harvested than for any other species. These redfish tag returns were primarily contributed by sports fishermen, but some were from trot line operators. In spite of the heavy fishing pressure, and even if the assumption is made that only 50 per cent of the recovered tags were turned in, fishing mortality for redfish is not over 30 per cent. Isolated schools of redfish, however, may have much greater mortality. In one instance April 24, 1951, 134 redfish from a single school were captured, tagged, and released. 22.3% were recovered, 80% within one year. If it is again assumed that 50 per cent of the recovered tags were turned in, the

TABLE 6

Comparison of tag recoveries for redfish and drum

Area	Redfish tagged	Recovered	Per cent recovered	Drum tagged	Recovered	Per cent recovered
Cedar Bayou	322	43	13.3	93	4	4.3
Aransas Bay	152	17	11.1	31	0=	0
Upper Laguna Madre (Year Class 0 only)	932	43	4.6	....	....	....
Upper Laguna Madre (All other Year Classes)	502	60	11.1	8,205	68	0.8
Baffin Bay	.....	....	.....	780	25	3.2
Lower Laguna Madre	155	6	6.0	....	....	....

fishing mortality would be about 50–60 per cent. 26 were recovered from sports fishermen; 4 were recovered from commercial fishermen.

Springer and Pirson (1958) stated that at Port Aransas, Texas, redfish are caught throughout the year but the peak months occurred in the fall when an outward migration occurred. Large catches were also reported in July and August. This is somewhat similar to the situation in the Laguna Madre where the fall and spring months are most productive. It is difficult to determine the actual number of redfish caught in the surf since so much of the beach is now accessible, but reported landings at Port Aransas of 6,964; 4,567; 9,644; 3,369 and 1,840 fish during the years of 1952, 1953, 1954, 1955 and 1956 are probably indicative of the catch along this beach.

Black drum were caught at Port Aransas throughout the year, but the best catches occurred from October to February with the highest peak in November. Catches of 1,974; 4,321; 4,055; 1,741 and 1,181 fish were noted for 1952, 1953, 1954, 1955 and 1956.

Although both redfish and drum are primarily bottom feeders, fishing techniques differ for the two species. Redfish are caught in potholes on the grassy flats, near oyster reefs, near passes, and occasionally in boat basins. In the Upper Laguna Madre and in some of the channels of the lower Laguna Madre small redfish are caught in the spring. However, the larger fish must be sought in the almost inaccessible shallow flats, particularly in the lower lagoon where fishermen use shallow draft boats to reach the fish.

In Baffin Bay redfish contribute a great deal to fishing enthusiasm. Due in part to the remoteness of the area and the difficulty of navigation, total sports landings are probably less than in other sections. Serpulid reefs are fished heavily and yield many fish, usually weighing from one to 15 pounds. Dead baits, normally cut mullet and shrimp tails, are commonly used, the water being too turbid for the artificial spoons used in the Laguna Madre and elsewhere.

Surf fishing with cut bait or lure, is common all along the Gulf beach and many mature redfish are captured in this fashion.

Black drum are usually taken with dead bait, either peeled shrimp or cut up fish, and most catches are on bottom rigs. These fish may be caught in deep channels or near the edges of shoals. Many large drum are caught each year in the Intra-coastal Waterway and in deep holes in Corpus Christi Bay, primarily by out of town or out of state fishermen who value them for their sheer size and weight. Surf fishing, using cut bait, also produces many fish.

Commercial Fishery

Commercial harvest of redfish and black drum is confined primarily to the gulf states although small landings are reported from the Atlantic coast. Only in Texas do landings of drum exceed those of redfish (Table 7). Data were derived from Anderson and

Table 7

Commercial landings of redfish and black drum by year and state

	In thousands of pounds									
	Florida		Alabama		Mississippi		Louisiana		Texas	
Year	Red	Drum	Red	Drum	Red	Drum	Red	Drum	Red	Drum
1887	.....	.....	.....	.....	.....	.....	.....	.....	838.7	.....
1888	.....	.....	.....	.....	.....	.....	.....	.....	772.5	.....
1890	.....	.....	.....	.....	.....	.....	.....	.....	1,107.9	4
1932	764	48	44	1	75	89	281	87	824	932
1934	1,017	100	65	1	73	4	493	199	1,579	2,253
1936	1,160	197	34	2	88	8	347	150	956	2,257
1939	1,081	84	39	3	165	26	694	150	471	1,320
1940	833	130	27	1	55	14	183	92	265	492
1945	2,053	986	250	65	2	20	596	301	1,297	1,213
1950	942	50	16	3	51	20	456	197	567	708
1951	919	36	44	11	31	8	384	235	238	702
1952	647	126	56	3	41	2	328	139	250	614
1953	526	71	46	2	62	5	273	64	511	770
1954	752	45	19	2	61	1	271	68	721	2,191
1955	754	48	19	3	57	14	344	128	494	1,972
1956	763	69	50	5	71	39	407	148	641	1,852
1957	667	62	10	2	54	21	353	184	504	1,502

Peterson (1952, 1953, 1954), Anderson and Power (1949, 1951, 1955, 1956a, 1956b, 1957), Collins (1892), Collins and Smith (1891), Fiedler (1938, 1940, 1941, 1943) and Townsend (1899).

Guest and Gunter (1958) noted that production of sea trout was fairly stable in Florida and this also is true for redfish and drum. Anderson and Peterson, 1952–54; Anderson and Power, 1949–1957. The major exception was during the war years when restrictions were lifted in the interest of a national emergency. All other Gulf states have had considerable fluctuation in landings.

In Texas, fluctuations have been caused by mass mortality from freezes, phytoplankton blooms, hypersalinity, opening and closing of bays to fishing by legislative action, and by economic considerations. Fig. 13 shows landings over a number of years and an attempt is made to correlate these landings with the factors mentioned. In 1890, Collins reported that fishing activity had increased greatly during the preceding ten years with many more men being employed. Most of the effort was apparently directed toward catching redfish. This trend was reflected for a number of years and it was not until 1918 that drum landings exceeded those of redfish. It was during that year that a national emergency brought about the sale of almost all types of fish caught. Unfortunately, data are very scarce during these early years. Landings appear to have been relatively stable from 1927 to 1932 with some slight decline in redfish capture. There was a substantial increase in fish caught in 1934, possibly correlated with an economic depression which drove people, normally employed elsewhere, into the fishing industry. In about 1935, a phytoplankton bloom described by Gunter (1952) destroyed many fish in the Gulf of Mexico and may have lowered catches of redfish accordingly.

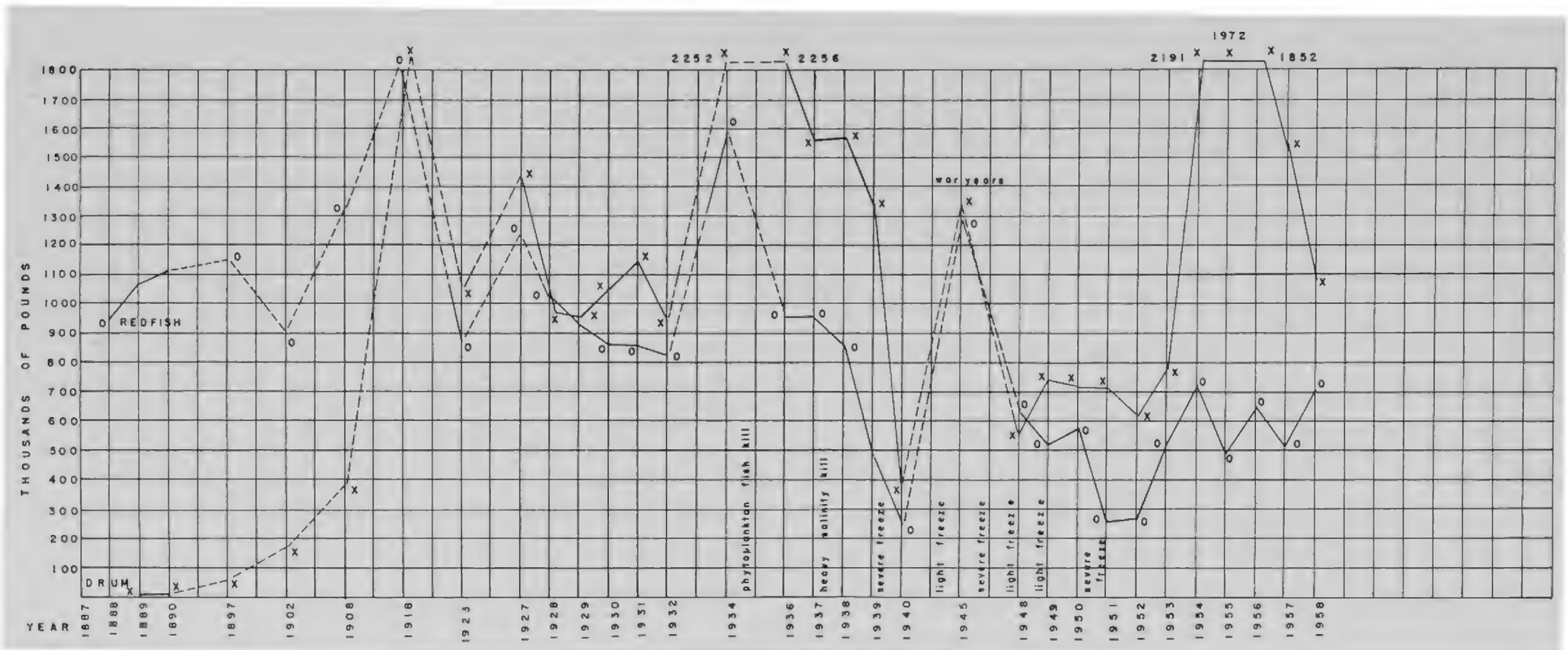

FIG. 13. Commercial landings, redfish and black drum, for the State of Texas; factors which influenced landings are indicated.

Hypersalinity in the Laguna Madre in the summer of 1937 killed many of the fish in that bay and the catch of redfish, and more notably drum, dropped accordingly during the next two years. Before populations had time to recover, the Texas coast was struck, in 1940, with one of the most severe blizzards in history. Gunter (1941) stated that water temperature fell to 39°F and there was considerable ice along the shore. Fish were packed in windrows all along the shores of the bays and millions of pounds were destroyed. Commercial landings fell to the lowest level in history. A minor kill due to freeze occurred in 1941, a heavy one in 1947 and other minor ones in 1948 and 1949. All of these tended to keep the level of landings below those of prior years. In late January, 1951 another severe blizzard struck the coast with air temperature from January 29 to February 3, of 25, 22, 22, 18, 20, and 19°F for consecutive days (Gunter and Hildebrand 1951). Dead fish were checked by Game and Fish Commission biologists immediately after this freeze and it was estimated that from 60 to 90 million pounds of fish were killed. This dropped redfish landings to a further low ebb but lowered drum landings very little.

Another factor influencing commercial fishing is legislative opening and closing of bays to net fishing. Most Texas bays, with the exception of the Laguna Madre, were closed in 1925 but several were re-opened at later dates. The Laguna Madre was closed by sections starting in 1931 with Cameron County being the last to close. In 1959 several large bays remained open but much of the perimeters of these bays and practically all of the shallow bays, where fishing with nets is most successful, were closed.

It must be noted that, as use of nets decreased use of trotlines increased. Breuer (unpublished data) conducted a survey a survey of trot line fishermen in the lower Laguna Madre and found that in September 1959, eight trot liners fished 24,500 hooks and caught 14,113 pounds of redfish and 5,131 pounds of black drum. In that area the mainline is suspended above the water between poles and the drops or stagings extend down with the hooks just under the water. The bait, usually a colored piece of plastic, is moved by waves and is effective in taking both redfish and drum. In the lower Laguna Madre this method is geared primarily for the taking of redfish with drum being caught incidentally. Supplemental lines, baited with live perch or cut fish, are effective in taking larger redfish and large trout. In the upper Laguna Madre, fishing is geared to the taking of drum with redfish incidental. Bottom lines, baited with shrimp, are often used as a supplement to high lines.

Mr. John R. Beasley, of Beeville, Texas has compiled the catch of redfish and drum by various means in 1956. These data presented show that nearly 34 per cent of the redfish and over 46 per cent of the drum landed commercially were taken on trot lines.

Commercial production of fish in Texas has changed in location completely since the turn of the century. At one time the Laguna Madre supplied less than two per cent of the commercial landings for Texas; since that time the Laguna has become the leading producer for the state. Table 8, compiled by Mr. Beasley, shows the catch for the Laguna Madre as compared to that of all the other bays in Texas.

The only time more drum were landed from any single bay than from the Laguna Madre was in 1956–57 and 1957–58 when heavy rainfall flushed out the lagoon and the fish spread into the Gulf and into the Aransas-Corpus Christi Bay area.

While the normal trot line procedure of commercial fishing may contribute significantly to a suitable harvest of redfish and while the percentage of black drum taken by

TABLE 8

Pounds of Redfish and Black Drum caught in the Laguna Madre as compared to the rest of the Texas coast for a period of 22 years. Compiled by J. R. Beasley, Beeville, Texas.

Year Year	Region Region	Redfish Redfish	Drum Drum	Totals Totals
1936–37	Laguna	373,357	1,227,200	1,600,557
	Bal. coast	288,217	348,705	637,022
1937–38	Laguna	345,581	1,330,901	1,676,452
	Bal. coast	416,076	777,991	1,194,067
1938–39	Laguna	229,772	993,649	1,123,421
	Bal. coast	181,074	464,418	645,465
1939–40	Laguna	142,998	507,187	650,185
	Bal. coast	141,181	117,597	258,778
1940–41	Laguna	94,453	421,158	515,611
	Bal. coast	119,661	58,268	177,929
1941–42	Laguna	517,806	627,844	1,145,650
	Bal. coast	223,092	110,409	333,501
1942–43	Laguna	598,708	963,779	1,562,487
	Bal. coast	368,339	133,198	501,537
1943–44	Laguna	382,033	786,578	1,169,611
	Bal. coast	448,116	153,422	601,538
1944–45	Laguna	432,120	783,299	1,215,419
	Bal. coast	511,434	216,448	727,882
1945–46	Laguna	314,553	689,617	1,004,170
	Bal. coast	417,549	508,633	926,193
1946–47	Laguna	304,713	454,578	759,291
	Bal. coast	185,696	203,836	389,532
1947–48	Laguna	212,839	219,009	431,848
	Bal. coast	249,413	221,744	471,187
1948–49	Laguna	309,227	363,735	672,962
	Bal. coast	158,761	168,653	327,414
1949–50	Laguna	170,401	222,521	392,922
	Bal. coast	304,067	322,047	626,114
1950–51	Laguna	101,532	429,436	530,968
	Bal. coast	199,882	161,301	361,183
1951–52	Laguna	79,663	290,319	369,982
	Bal. coast	199,882	161,301	361,183
1952–53	Laguna	131,869	406,922	538,791
	Bal. coast	227,256	261,948	489,204
1953–54	Laguna	223,039	262,701	485,740
	Bal. coast	176,065	132,855	308,204
1954–55	Laguna	328,520	838,195	1,166,715
	Bal. coast	125,553	146,563	272,126
1955–56	Laguna	292,962	609,358	902,320
	Bal. coast	124,505	140,655	265,160
1956–57	Laguna	208,153	465,939	674,092
	Bal. coast	158,092	832,439	990,531
1957–58	Laguna	237,280	134,094	371,374
	Bal. coast	195,633	500,091	695,724
TOTALS	Laguna	6,031,579	13,028,019	19,239,598
	Bal. coast	5,333,295	6,189,053	11,523,148

TOTAL SEA TROUT, REDFISH AND BLACK DRUM: 49,310,841
ESTIMATED LOSS IN 1951 FREEZE: 60,000,000–90,000,000

this method may amount to a significant portion of the total commercial bay catch, this fishing procedure cannot begin to approach a suitable harvest of the total available black drum population.

The black drum population of the Laguna Madre is extensive and since the normal feeding habits of drum are considered to be detrimental to important vegetation of the area, a program designed to effect a suitable drum harvest has been initiated in the lower Laguna Madre. In 1957, the bay waters of Cameron County were opened to contract

commercial fishing for drum during the months of December, January and February of each year using accepted gill nets. In 1959, Willacy County joined with Cameron County but for the months of January through May of each year. Under this program, contracts are let by the Game and Fish Commission to persons for the express purpose of taking black drum from the bay waters of these counties. Hours of operation, gear to be used, keeping of records and license requirements are governed by strict rules and regulations. These are agreed to by the contract applicants before the contract is let, to minimize any adverse effects on other species of marine life and to vegetation and bay bottoms. The program was recommended to improve and to decrease the detrimental effects caused by an overabundant drum population.

Summary

1. Data on two of the most important food and game fishes of the Texas coast, the redfish and the black drum, are summarized.

2. Redfish range from New Jersey on the Atlantic to Tuxpan, Mexico in the Gulf of Mexico. Drum are found from New York to as far south as South America.

3. Spawning of redfish occurs in the Gulf of Mexico, possibly near passes, in fall months. Young fish move through passes into the bays which serve as nursery grounds.

4. Growth is rapid; standard lengths of 320, 530, and about 700 mm being reached in the first, second and third years.

5. Food consists primarily of various crabs, fishes and shrimp. As size of the redfish increases the percentage of crabs eaten also increases.

6. There is little movement of these fishes between bays and even less between bay and gulf. Apparently some redfish move to the gulf when less than one year old and never re-enter bays. There are minor movements each day between feeding grounds and deeper water.

7. Redfish are euryhaline but are most often found at 20–45 ‰. Considerable fluctuation in temperature is tolerated if changes are gradual but many fish are destroyed by sudden cold spells.

8. Spawning of the black drum occurs in and near passes and in many shallow bay areas. While 90 per cent of the spawning occurs in February and March, some spawning has been noted as early as December with a secondary spawning in May and June. Milt and eggs are dropped in any location while schools of fish are moving. Spawning and nursery grounds can be the same location.

9. Standard lengths of 160, 310 and 415 mm in one, two, and three years respectively, are attained. Beyond the third year, growth continues at the rate of 50 mm per year.

10. Food of the black drum consists principally of small mollusks, crabs and vegetation with lesser amounts of shrimp, polychaete worms, and small fish being consumed.

11. There is little movement of drum from bay to bay or from bay to gulf.

12. While the black drum is capable of tolerating almost any salinity range encountered from 10 to 85 ‰, the usual range is 25 to 50 ‰. Temperature fluctuations can be tolerated if they are not too rapid, too severe or too prolonged.

13. Both redfish and drum are parasitised extensively by the "spaghetti worm" and to a lesser degree by copepods and isopods.

14. Redfish are sought by most sport fishermen and creel census data indicates a

harvest of about one million pounds per year for bay areas. Drum are sought less extensively.

14. Due to the bottom feeding habits of both fish, most are captured on dead bait or sub-surface artificial lures. Tag returns show that a much larger per cent of the total population of redfish is harvested than of drum.

15. Both redfish and drum are taken commercially by nets, trot lines and rod and reel. Since legislative closure of bays to net fishing, the use of trot lines has been intensified. From a position of little commercial importance, the Laguna Madre has become the leading area in commercial landings. Fluctuations have been caused by such factors as mass mortality from freezes, hypersalinity and by the opening and closing of bays to nets.

16. Total commercial landings for trout, redfish and drum for the last 22 years in Texas were just under 50 million pounds while the mortality from the freeze of 1951 alone was 60 to 90 million pounds. Since 1936, the average annual commercial landings on the Texas coast have been 516,585 pounds of redfish and 873,544 pounds of drum.

17. Drum population recovered from freezes more rapidly than redfish and within two years overpopulations existed. Overpopulations tended to be detrimental to redfish, trout and brown shrimp as the normal feeding habits of drum destroy vegetation which serves as spawning and nursery grounds for these species. In an effort to alleviate overpopulation, rough fish permits for drum only, have been issued for certain parts of the Laguna Madre.

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Sedimentation From a Hydraulic Dredge in a Bay[1]

THOMAS R. HELLIER, JR.[2] AND LOUIS S. KORNICKER[3]

Abstract

Red gravel was used to mark the bay sediment surface at 5 stations in turtle grass flats near Aransas Pass, Texas prior to the dredging of an intracoastal waterway. Cores were taken and sediments were studied before, one week after dredging, and 18 months later. 22 to 27 cm of sediment (11 to 55% silt-clay) were deposited within 0.5 mile of the dredge, but effects at greater distance were negligible. Little sediment sorting was observed during dredging.

Introduction

It is routine in the digging of channels in Texas bays and lagoons for a hydraulic dredge to deposit sediment removed from channels in discrete piles called "spoil islands" or "spoil banks." The objective of the present study was to ascertain the amount of sediment distributed on a shallow fertile bay bottom as a result of sediment by-passing the spoil island during the dredging operation, and by lated erosion of the spoil island. The work was part of a joint project by the Texas Game and Fish Commission of Texas and the Institute of Marine Science, designed to determine the effect of dredging on marine life. The area chosen for the study was Redfish Bay, near Aransas Pass, Texas. A "before and after" type study was possible because of a projected extension of the intracoastal canal, 125 feet wide and 12 feet deep, through Redfish Bay.

The method used to estimate the amount of sediment deposited in the bay by the dredge was as follows: square meter quadrats were marker off in five locations over the turtle grass flats in Redfish Bay by setting a bamboo pole, easily visible from a distance, at each corner of a quadrat. A layer of red aquarium gravel was then spread on top of the sediment inside the quadrats. Cores were then collected periodically before and after dredging from within each quadrat, and the thickness of sediment above the red gravel measured. Plastic tubes 1⅝ inches in diameter were used for coring.

The five quadrats were oriented perpendicular to the proposed channel (Fig. 1). The channel was dug between quadrat 1 and the mainland. Quadrat 1 was approximately 0.03 mile from the channel, quadrat 2 was 0.5 mile, quadrat 3 was 1.0 mile, quadrat 4 was 1.5 miles, quadrat 5 was 2.0 miles distant from the channel. The spoil from the channel was deposited between quadrats 1 and 2, but closer to 1 than 2.

Results

Cores obtained immediately after the red gravel was spread on the sediment were kept in the laboratory as controls in order to determine whether or not the gravel would sink by its own weight into the sediment. The gravel remained on top of the sediment

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FIG. 1. Photograph facing south along the intracoastal channel after the dredging in May, 1960. Station 1 is indicated in the middle right. Station 2 is along the left margin. Stations 3–5, not visible, stretch out to the left (west) of the spoil island more or less perpendicular to the channel axis. Dark areas underwater behind the spoil island are grass flats. The causeway between Aransas Pass and Port Aransas is visible in the background. The narrow strip of land covered with vegetation in the foreground is man-made, once supporting a railroad. The picture was taken by Mr. W. Garner from a U. S. Army helicopter.

in the coring tubes throughout the tests. Slight agitation simulating wave action in the tubes did not cause the gravel to sink into the sediment.

In September, 1959, nine months after the gravel was distributed, the quadrats were re-cored in order to estimate thickness of sediment deposited in the bay under existing conditions prior to dredging. The amount of sediment deposited during the nine month period was negligible at all 5 quadrats, being at most 2–3 mm. The quadrats were again re-cored about one week after the dredge passed through the sample area. Twenty-seven cm of sediment were deposited over quadrat 1, and 22 cm over quadrat 2 (Table 1). Sediment deposited on quadrats 3, 4, and 5 was negligible.

Eighteen months after the dredge had passed the sample area the quadrats were again

TABLE 1

Amount of sediment deposited before and after dredging*

Station quadrat no.	Thickness of sediment deposited in 9 months prior to dredging, cm	Thickness of sediment 1 week after dredging, cm	Thickness of sediment 18 months after dredging, cm
1	negligible	27	32
2	negligible	22	33
3	negligible	½	negligible
4	negligible	½	----
5	negligible	½	3

* Thickness of sediment measured from reference surface marked with red gravel spread in December, 1958.

re-cored in order to estimate the amount of sediment that had been distributed on the bottom as a result of erosion of the spoil island. The gravel in quadrat 1 was found to be covered with 32 cm of sediment and in quadrat 2 with 33 cm showing that 5 cm of sediment had been added to quadrat 1 and 11 to quadrat 2 as a result of erosion of the spoil island. Sedimentation on quadrat 3 was negligible; quadrat 4 could not be located. Quadrat 5 had 3 cm of organic muck over the gravel, but this apparently was not derived from the spoil island.

In order to ascertain how the composition of the sediment was affected by dredging, the upper 10 cm of sediment in quadrats 1, 2, 4, and 5 were separated into a silt-clay and shell-sand fraction before the dredging by sieving (Table 2). The sieving was re-

TABLE 2

Composition of sediment before and after dredging

Station no.	Miles from dredge	Before dredging silt-clay per cent*	One week after dredging silt-clay per cent*
1	0.03 west	51	11
2	0.5 east	43	55
3	1.0 east	60	60
4	1.5 east	...	
5	2.0 east	67	67

* Remaining percentage of sediment consisted of sand-shell fraction.

peated with the sediment deposited by the dredge in quadrats 1 and 2. The sediment deposited by the dredge in quadrat 1 was coarser than the original, containing only 11 per cent of silt-clay mixture compared to 45 per cent before dredging (Table 2). The sediment deposited on quadrat 2 was not appreciably different from the underlying sediment. The sediment deposited on quadrats 1 and 2 during the dredging operation was homogenous with no layers apparent. Sediment deposited during post-dredging erosion of the spoil island was finer than that deposited during the dredging (R. Schultz, personal communication, 1960).

Discussion and Conclusions

Ingle (1952) found after studying sediment deposition during dredging in a Florida bay that damage caused by deposition of mud on the bottom did not extend beyond 0.23 mile from the dredge. In Redfish Bay dredged sediment was deposited more than

0.5 mile, but less than 1 mile, from the spoil bank, somewhat further than Ingle observed in Florida.

It might have been erroneously predicted that during the dredging operation dredged sand and shell would remain on or close to the spoil area, and clay and silt spread widely on the bay bottom. The similarity in the composition of sediment before and one week after dredging on quadrat 2 and non-deposition of sediment appreciably further than 0.5 mile from the spoil area indicate that the sediment was not sorted to an appreciable extent during the dredge operation. This may be because sediment containing clay is usually ejected from the dredge flume as chunks (mud balls) rather than as discrete particles (Kornicker, Oppenheimer, Conover, 1959). Some sorting locally is indicated by the low percentage of the silt-clay fraction in sediment deposited on quadrat 1 during dredging.

The accumulation of sediment finer than the original on quadrats 1 and 2 during the 18 months following the dredging indicates that sediment forming the spoil island is sorted as it is reworked by waves. It might be predicted that sediment surrounding the spoil area will become somewhat coarser as the finer material is removed and distributed in deeper water.

The fact that more sediment was deposited during the 18 month post-dredging period on quadrat 2 (11 cm) than on quadrat 1 (5 cm) suggests that waves are the principal agent eroding the spoil bank, since station 2 faces the windward side of the spoil island, whereas station 1 faces the lee side.

The accumulation of more sediment on the windward side of the spoil island than on the lee side during the post-dredging period suggests that spoil islands formed during dredging should be situated on the windward side of channels from which the sediment was obtained in order to minimize the amount of sediment returning to the channel.

The technique of using colored gravel chips as a reference to gauge deposition of sediment proved workable and may be useful for making similar studies elsewhere.

Acknowledgments

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Shrimp Landings and Production of the State of Texas for the Period 1956-1959, with a Comparison with other Gulf States[1]

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Abstract

Data on shrimp production from 1956 through 1959 in Texas and other states of the Gulf and South Atlantic area are presented in tables and graphs from state and federal sources. Interpretive comments are made on trends, seasonal variations, and areal differences. In Texas total production has been relatively stable but white shrimp production has declined. White shrimp dominate landings in Louisiana and the upper Texas coast; brown shrimp dominate the catch of the central Texas coast; while pink shrimp are important in Florida and the lower Texas coast. Following maximum yields of brown shrimp in summer and white shrimp in the early fall, catch records show a southward drift of populations off the Texas coast in fall. Catch per hour was correlated with total production and was markedly seasonal.

Introduction

A few years ago the United States Fish and Wildlife Service introduced a better and more complete system of collecting production statistics on the shrimp fishery. This program was carried on in collaboration with the various states. These statistics and some earlier ones collected by the Texas Game and Fish Commission were utilized in this assessment of the present production of the shrimp fishery of Texas. The concern is with landings and production and not with price variations and other economic factors.

The Marine Products Reports and previous annual statistics of the Texas Game and Fish Commission, which were used only briefly for comparison with former years, have been published in the various Annual Reports of the Game and Fish Commission extending back for almost forty years. They are not cited. The federal figures used are from work sheets furnished by the Fish and Wildlife Service to the Marine Laboratory of the Game and Fish Commission at Rockport, Texas (Table 1). These differ slightly from the figures published in the annual Fishery Statistics of the United States. Both sets of data are on file at Rockport.

The following account refers to landings of the United States Gulf of Mexico coast, and more briefly to the south Atlantic coast. The minor Pacific coast shrimp fishery is not considered.

[1] Contribution No. 54 from The Marine Laboratory of the Texas Game and Fish Commission.
[2] Present Address: Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

TABLE 1

Gulf shrimp landings in pounds, heads-off

Year		Florida	Alabama	Mississippi	Louisiana	Texas	Grand total
1956	Brown	556,997	3,067,848	6,095,390	12,123,228	33,179,663	55,023,126
	Pink	28,013,357	261,920	200,400	765	496,281	28,972,723
	White	617,399	1,249,945	2,355,629	17,131,580	3,135,661	24,490,214
	Seabobs	47,433	.....	250	828,647	79,442	955,772
	Total	29,235,186	4,579,713	8,651,669	30,084,220	36,891,047	109,441,835
1957	Brown	707,137	2,993,847	5,673,824	11,120,068	43,136,212	63,631,088
	Pink	23,155,810	188,302	354,302	46	138,908	23,837,368
	White	881,161	410,417	957,084	6,581,743	2,298,533	11,128,938
	Seabobs	207,985	.....	.....	325,190	117,040	650,215
	Total	24,952,093	3,592,566	6,985,210	18,027,047	45,690,693	99,247,609
1958	Brown	1,024,035	2,261,455	2,972,957	8,324,163	36,669,887	51,252,497
	Pink	24,539,434	68,906	103,754	294,383	9,876	25,016,353
	White	1,573,384	829,212	1,512,567	14,454,824	7,369,827	25,739,814
	Seabobs	9,919	.....	.....	845,672	243,214	1,098,805
	Total	27,146,772	3,159,573	4,589,278	23,919,042	44,292,804	103,107,469
1959	Brown	953,254	3,795,381	5,457,779	16,143,481	43,428,838	69,778,733
	Pink	17,352,690	2,193	168,900	1,495	937,968	18,463,246
	White	755,230	974,276	1,894,192	15,172,218	5,761,192	24,557,108
	Seabobs	136,822	476	375	2,037,796	178,270	2,353,739
	Total	19,197,996	4,772,326	7,521,246	33,354,990	50,306,268	115,152,826

Shrimp Landings of Texas and other Gulf States

SHRIMP LANDINGS AT UNITED STATES GULF PORTS

During the years 1956 to 1959, inclusive, the United States Gulf landings of shrimp tails were 426,950,352 pounds. Shrimp with the heads off were multiplied by a factor of 1.68 to obtain the whole weight. The United States Gulf landings of whole shrimp during this four year period were 717,276,771 pounds. It should be noted that these figures represent more than the total production of the Gulf states, for some of the shrimp were caught outside of territorial waters of the United States. Similarly, the figures are less than the total production figures for the Gulf of Mexico, for the figures on Gulf shrimp landed in Mexico and Cuba were not available.

The United States landings during the same four year period, including the South Atlantic states, were about 820 million pounds in terms of whole shrimp, with an average of about 205 million pounds a year. The South Atlantic production comes from North and South Carolina, Georgia, and the Atlantic coast of Florida. Due to the high price of the product, the shrimp fishery was the most important one in the United States, exceeding any of the others in value, such as the menhaden fishery, although in 1956 and again in 1959 over two billion pounds of menhaden were landed.

During the 1956–1959 period the Gulf landings of headed shrimp fluctuated from a low of 99 million pounds in 1957 to a high of 115 million pounds in 1959, with an average of slightly less than 107 million pounds a year. The figures are shown in Fig. 1.

LANDINGS BY STATES

The annual Texas landings of heads-off shrimp during the four year period varied from a little less than 37 million pounds in 1956 to over 50 million in 1959, with an

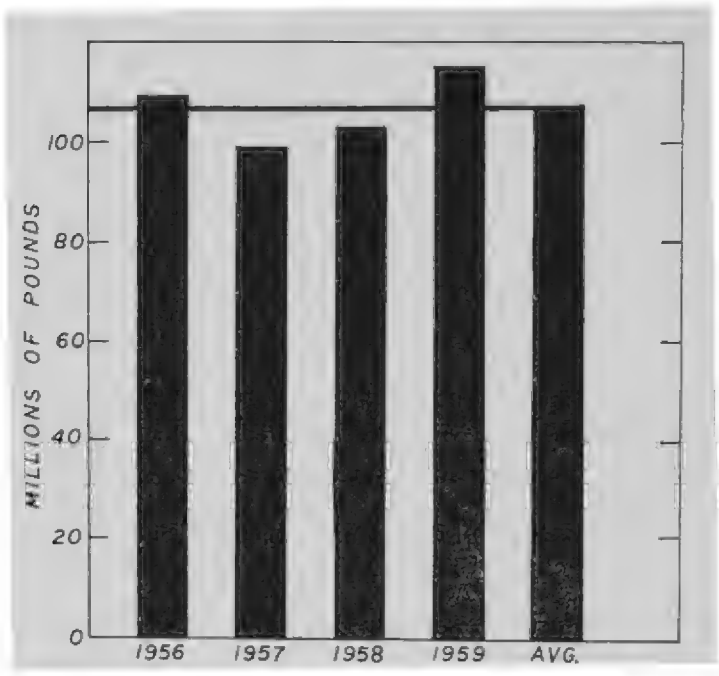

FIG. 1. Total landings of headed shrimp at United States Gulf Coast ports, 1956–1959.

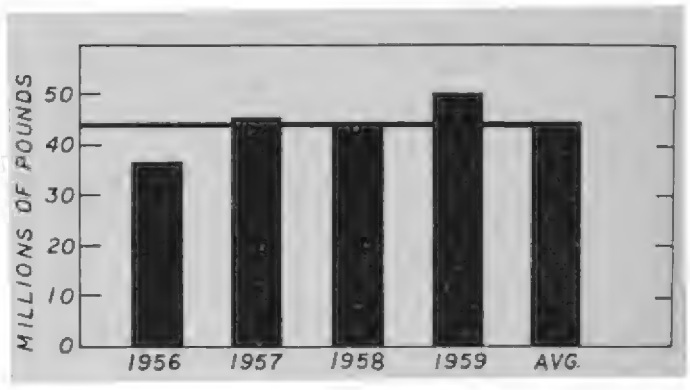

FIG. 2. Total landings of headed shrimp at Texas ports, 1956–1959.

average of over 44 million pounds a year. Texas landings were 41.5 per cent of the Gulf landings during this period. The figures are given in Fig. 2.

Table 1 shows the variations in landings of heads-off shrimp for the several Gulf States, with averages and percentages. Several interesting facts are apparent. The Texas shrimp fishery is larger than that of any other state in the Union. Texas, Louisiana and Florida are the states with high landings and 90 per cent of the Gulf Coast landings come into ports of these three states. The remaining 10 per cent goes into Mississippi and Alabama ports. Louisiana and Florida landings are almost equal, but Louisiana stands higher as a producer than is shown in the table, because a considerable proportion of the Mississippi and Alabama landings are caught in Louisiana waters. Furthermore, a considerable proportion of Texas and Florida landings come from the Campeche Banks, but Louisiana landings come primarily from waters of that state.

Among the high producing states, the Louisiana landings fluctuated most from the averages, 32.0 per cent, and Texas landings fluctuated least, 16.7 per cent. Florida landings fluctuated 23.6 from the mean. These facts are noted here because stability of landings is of great importance to the industry.

Table 1 also shows that 1959 was the year of highest landings for Texas, Louisiana and Alabama and 1956 was the best year for Florida and Mississippi.

Figure 3 shows graphically the average annual heads-off shrimp landings of the various Gulf states for the four year period.

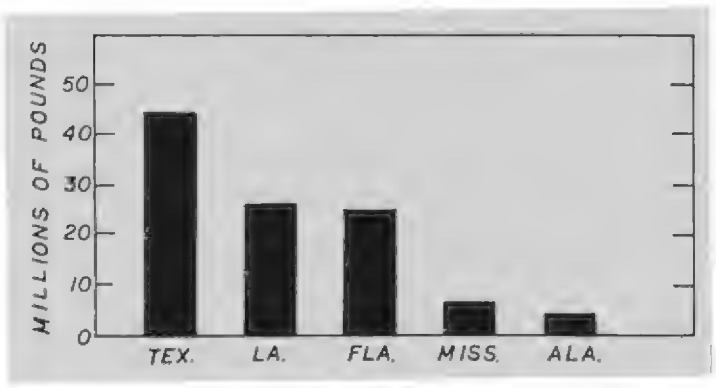

FIG. 3. Average annual landings of headed shrimp of the Gulf States, 1956–1959.

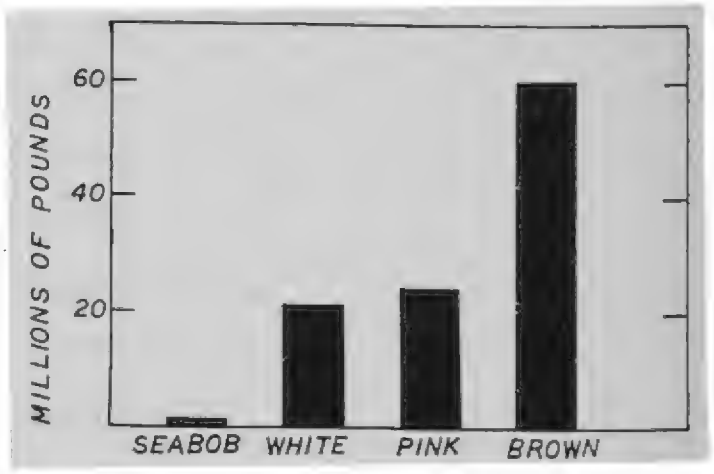

FIG. 4. Average annual production of headed Gulf shrimp by species, 1956–1959.

Landings by Species

Four species of shrimp are fished commercially in the Gulf of Mexico. The annual average landings at Gulf ports in pounds of headed shrimp for the four year period were: seabobs (*Xiphopeneus kroyeri*) 1,264,633 (1.2 per cent); white shrimp (*Penaeus fluviatilis*) 21,479,019 (20.1 per cent); pink shrimp (*Penaeus duorarum*) 24,072,423 (22.5 per cent); brown shrimp (*Penaeus aztecus*) 59,921,361 (56.2 per cent). These figures are shown graphically in Fig. 4. During the period under discussion Mississippi and Alabama landed only 1,101 pounds of seabobs. Florida averaged 100,540 pounds, or 8.0 per cent of the Gulf landings; Texas averaged 154,492 pounds or 12.2 per cent, and Louisiana averaged 1,009,326 pounds, or 79.8 per cent of the annual Gulf catch of the species.

In Texas the average seabob landings for the four-year period amounted to slightly more than 0.3 per cent of the state total of shrimp landings, and in Florida the percentage was only 0.4. Actually, the seabob is of importance only to the State of Louisiana, where it amounted to 3.8 per cent of the total shrimp landings. In 1959, seabob landings were 6.1 per cent of the Louisiana total. Seabobs are generally caught in United States waters, but they are not of much importance to Texas, and make up only about 1.2 per cent of the Gulf landings for the four-year period.

In 1956–59 Florida landings of pink shrimp amounted to 23,265,323 pounds a year or 96.6 per cent of the Gulf pinks. Texas was second with 395,558 pounds a year or 1.6 per cent of the Gulf total. Mississippi, Alabama and Louisiana trailed in pink shrimp landings with less than 1.0 per cent each. The average annual landings for these three states were: 206,839, 130,330 and 74,172 pounds, respectively. Florida dominates the pink shrimp landings in the Gulf of Mexico and that shrimp is of little importance to the other states.

The average annual landings for the period 1956–59 of pink shrimp, white shrimp and brown shrimp are given by states in Table 2.

Louisiana led in white shrimp landings and Texas led in brown shrimp landings. The white and brown shrimp are of little importance to Florida, but they are of major importance to the other Gulf states. Texas ranks first in landings of the browns and sec-

Table 2

Annual average landings of heads-off pink, white and brown shrimp for all Gulf states for the period 1956–59, inclusive, with percentages

	Pink shrimp				
	Florida	**Texas**	**Mississippi**	**Alabama**	**Louisiana**
Annual landings	23,265,323	395,578	206,839	130,330	74,172
Gulf percentage	96.6	1.6	0.9	0.6	0.3
	White shrimp				
	Louisiana	**Texas**	**Mississippi**	**Florida**	**Alabama**
Annual landings	13,335,091	4,641,303	1,679,868	956,794	865,963
Gulf percentage	62.0	21.6	7.8	4.5	4.0
	Brown shrimp				
	Texas	**Louisiana**	**Mississippi**	**Alabama**	**Florida**
Annual landdings	39,103,675	11,927,735	5,049,988	3,029,633	810,356
Gulf percentage	65.2	19.9	8.4	5.1	1.4

ond for each of the other three shrimp (seabobs, pinks and whites). Louisiana ranks first in landings of whites and seabobs, second in browns and last in pinks.

The average annual shrimp landings in Texas by species are given in Table 3 with percentages of the State total. It is clear that Texas shrimp problems are concerned mostly with the brown and white shrimp.

TABLE 3

Average heads-off shrimp landings of Texas by species for the period 1956–1959

	Annual landings	Percentage
Brown shrimp	39,103,650	88.3
White shrimp	4,641,303	10.5
Pink shrimp	395,758	0.9
Seabobs	154,492	0.3
Total	44,295,203	.....

Texas Shrimp Production

Actual production figures of shrimp taken in Texas waters from 1956–59 ranged from 24,873,550 to 34,399,946 pounds of headed shrimp, and averaged 30,264,927 pounds annually. Table 4 shows that Texas produced an average of 68.3 per cent of the shrimp landed in the State, and 31.7 per cent or 14,030,003 pounds a year came from waters outside the State.

TABLE 4

The average annual catch of headed shrimp in Texas water for the years 1956 to 1959, inclusive, compared to shrimp landed from out of state

	State waters		Out of state	
	Pounds	Per cent	Pounds	Per cent
Seabobs	359	0.2	154,133	99.8
Pinks	32,040	2.0	1,550,993	98.0
Whites	4,118,210	88.7	523,093	11.3
Browns	26,114,318	66.8	12,989,357	33.2
Total	30,264,927	68.3	14,030,003	31.7

It is also clear from Table 4 that Texas waters produce few seabobs and few pinks, Probably the seabobs and white shrimp come from Louisiana waters, and the out of state browns and pinks from other waters of the western Gulf. Table 4 also shows that the brown and white shrimp make up 99.9 per cent of the Texas shrimp catch, the browns amounting to 86.3 per cent of the total and the whites amounting to 13.6 per cent.

The average annual white shrimp production for this period was slightly less than 7 million pounds of whole shrimp. During the 1930's the annual shrimp production of Texas averaged 12.3 million pounds of whole shrimp—these were entirely white shrimp, which was the only species fished at that time. In the 1940's the white shrimp production averaged 18.3 million pounds a year. During the late 1940's the brown shrimp fishery was begun. In 1950 Texas produced 12.7 million pounds of whole white shrimp, but the next year the catch fell off, and for the years in which we have statistics (1951, 1952, 1956 to 1959) the average annual production of whole white shrimp was only

6.7 million pounds, about half what it was in the 1930's and slightly more than a third of what it was in the 1940's.

There are several possible explanations of this decline in the white shrimp catch. For one thing, after the brown shrimp fishery got started in 1947 larger boats were built and the fishermen put more effort into Gulf fishing, which is in general devoted to the brown shrimp. They have never returned to bay fishing on the scale of the 1940's. However, shrimp fishermen turned to brown shrimp because the white shrimp declined in parallel with the greatest drouth this country has ever known. This drouth began in 1947 and became worse in the 1950's and was not broken until the spring of 1957. It is interesting to note that the average annual production of white shrimp in 1958–59 jumped to 9,852,000 pounds of whole shrimp, as compared to 3,985,000 for the previous two years. The increase was about 125 per cent following the rains. The writer has previously shown that Texas shrimp production is correlated with rainfall of the State, especially that of the same year and the two previous years (Gunter & Hildebrand, 1954).

However, there are other changes which tend to cause the decline in shrimp production shown in the statistics, especially in the bays where mostly white shrimp are caught. The relatively recent production of powerful outboard motors has led to the acquisition of hundreds of small cabin cruisers by sports fishermen. These people buy bait shrimp licenses and do their own trawling, not only for bait but for edible shrimp. The bait shrimp fishery has increased greatly, too, and these shrimp are not reported in the commercial catch. Chin (1960) showed that the two-year catch of bait in Galveston Bay amounted to 676,000 pounds. During the same period the commercial shrimp catch in Galveston Bay was 1,537,257 pounds. Not all of the shrimp reported were white shrimp, but the majority of them were.

White shrimp production along the Texas coast has certainly fallen sharply in the past ten years, and the fishing for shrimp is probably as heavy as it ever was, and is increasing. These facts highlight the necessity for adequate information on the causes of the decline and laws to protect the shrimp.

Texas Shrimp Catch by Areas

The Texas coast was divided into four areas for the purpose of collecting statistics on shrimp catches. Area 18 extends from the Louisiana line to north of Freeport. It includes the area offshore from Galveston Bay. Area 19 includes the Gulf area south of Freeport and the waters offshore from San Antonio, Aransas, and Copano bays. Area 20 includes the area of Corpus Christi Bay and the upper Laguna Madre. Area 21 extends outside the lower Laguna to Mexico. These areas are shown in Fig. 5.

As was noted before, the seabob is produced primarily in Louisiana waters. Therefore, it is not surprising to find that all but 12 pounds of the Texas seabob catch came from Area 18, which borders Louisiana. The average catch for the whole coast was only 359 pounds a year.

Table 5 gives the average annual catch of pinks, white and brown shrimp for the four areas described above. Sixty per cent of the pink shrimp were taken from Area 20, which lies off Corpus Christi Bay and the upper Laguna Madre. Over eighty-two per cent of the white shrimp were taken from there, northward and eastward, to the Louisiana line in Areas 19 and 18. Brown shrimp were taken all along the coast but were caught

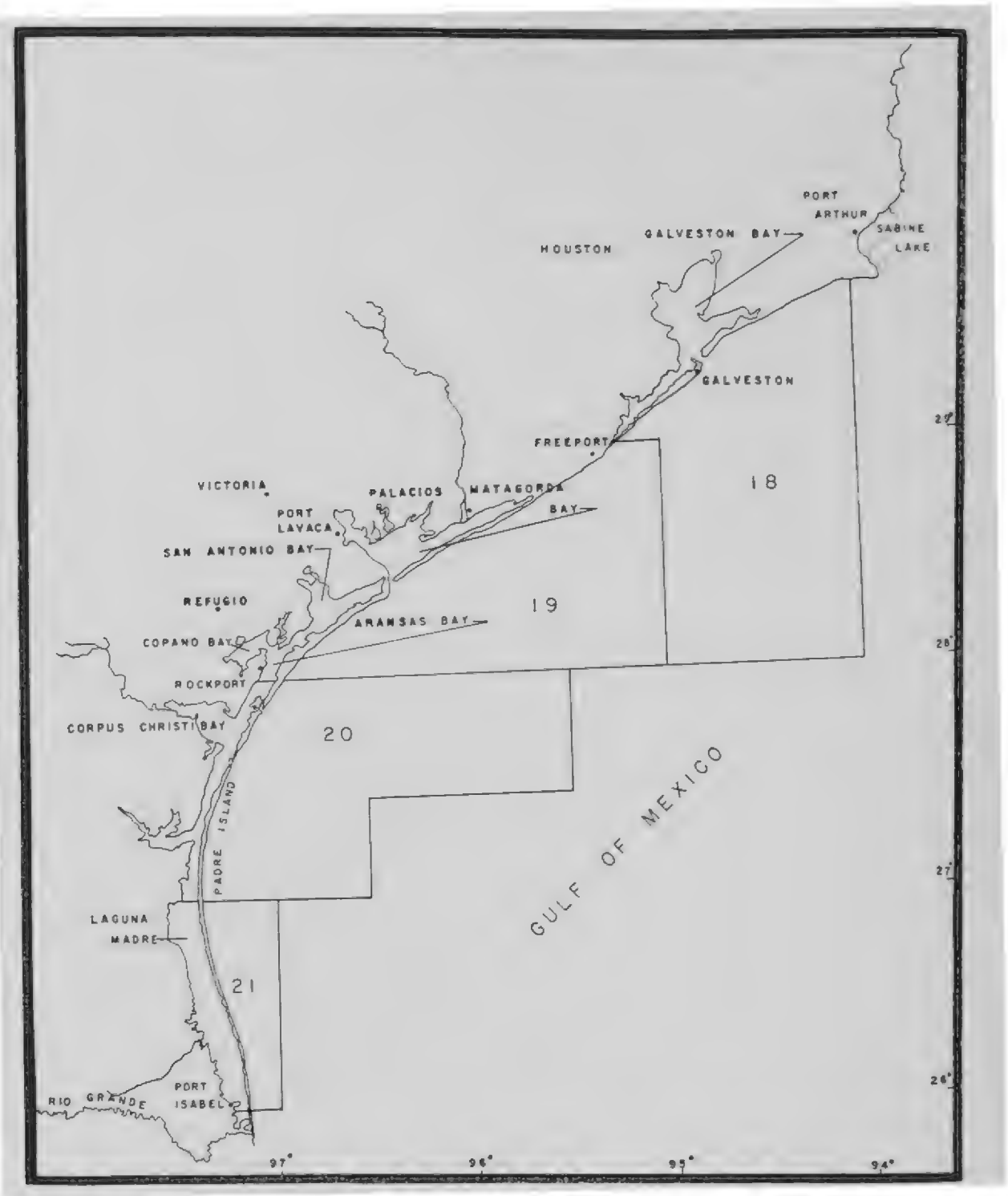

FIG. 5. Four areas used for comparing shrimp statistics along the Texas coast.

TABLE 5

The average annual catch by species of shrimp from the four areas of the Texas coast, for the years 1956–1959, in pounds of heads-off shrimp

Area	18	19	20	21
Pink	4,947	4,657	19,223	3,212
Whites	1,488,123	2,290,328	302,216	37,634
Browns	4,984,640	9,199,973	8,237,424	3,692,266

more than twice as abundantly in the two middle areas (19 and 20) as in the other two—the catch from these two areas being 66.2 per cent of the Texas total.

Table 6 gives the average monthly catch of the whole coast for pink, white and brown shrimp.

Almost half of the pink shrimp were taken in June, and 94.3 per cent of the catch was taken in the months of April to July.

TABLE 6

The average monthly production of heads-off shrimp by species of the Texas coast for the four year period, 1956–1959. Figures are in pounds.

Areas	January	February	March	April	May	June	July	August	September	October	November	December
Pinks	31	.....	603	2,334	8,369	15,356	4,154	125	.....	697	308	65
Whites	11,380	2,181	23,051	84,466	249,421	66,233	42,356	319,275	1,405,323	1,202,032	525,771	186,190
Browns	556,046	430,212	377,514	341,742	588,012	1,430,524	4,722,558	5,742,581	5,136,878	4,159,394	1,707,868	921,031
Total	567,457	432,393	401,168	428,542	845,802	1,512,113	4,769,068	6,061,981	6,542,201	5,362,123	2,233,947	1,107,286

TABLE 7

The average monthly production of heads-off white shrimp for the four areas of the Texas coast for the period, 1956–1959.

Areas	January	February	March	April	May	June	July	August	September	October	November	December
18	3,743	1,876	7,203	15,116	26,431	24,623	9,802	65,503	513,502	570,740	216,901	32,183
19	6,396	240	14,259	63,619	176,979	29,771	29,114	237,676	774,123	573,415	265,549	119,150
20	627	65	1,575	5,140	38,132	9,475	3,436	16,096	106,217	57,774	37,760	25,922
21	615	0	14	590	7,879	2,365	0	0	11,481	103	5,562	8,936
Total	11,381	2,181	23,051	84,465	249,421	66,234	42,352	319,275	1,405,323	1,202,032	525,772	186,191

TABLE 8

Monthly production of heads-off brown shrimp from the four statistical areas from north to south. The figures are averages of the four years, 1956–1959.

Areas	January	February	March	April	May	June	July	August	September	October	November	December
18	31,902	27,954	22,401	21,138	37,639	210,367	1,205,296	1,425,423	709,476	1,046,588	196,736	49,715
19	125,054	60,616	106,012	103,814	270,664	359,449	1,524,638	2,301,824	1,778,108	1,762,593	526,876	280,317
20	223,648	204,900	141,816	121,417	166,794	698,410	1,231,140	1,590,739	1,762,659	1,014,850	695,146	374,946
21	175,439	136,741	107,283	95,373	101,908	162,297	761,486	424,594	886,635	335,363	289,112	216,052
Total	556,043	430,211	377,514	341,742	588,012	1,430,523	4,722,560	5,742,580	5,136,878	4,159,394	1,707,870	921,030

September was the month of the greatest white shrimp catch and 63.3 per cent of the Texas catch was made during the months of September and October; 84 per cent of the catch fell in the four months of August to November. The only other month of sizable production was May, which is apparently a reflection of the spring run that appears in some years.

August was the month of greatest production of brown shrimp, and almost 74 per cent of the brown shrimp catch was in the months of July to October.

When the total shrimp catch is considered it is seen that March and April are the months of lowest production, only 3.2 per cent of the annual total being taken in those months. In contrast ,40.0 per cent of the catch was taken during August and September, and 73.3 of the total catch was taken in the four months July to October.

Table 7 shows the average white shrimp production by months for each area during the four-year period. February was the low month in all areas. The spring increase in production began to show in March and reached a peak in May in each area. This is the well known "spring run" of the fishermen. Another interesting fact concerns the fall fishery. In every area, except 18, there was a decrease from September to October, and in all areas there was a decrease from September to December, and the percentage decrease was less from north to south.

The percentage declines from September to December for the four areas, 18, 19, 20 and 21 (from north to south) were 93.7, 84.6, 75.4, and 22.3, respectively. The percentage changes are even greater if we consider the period October to November. During that period, the trend reversed in the southernmost area and the catch increased from October to December. The percentage changes in catch for this period for the area from north to south are: —94.4, —79.1, —55.0 and 8,675.0. The only reasonable explanation of this set of figures is that, after the shrimp go into the Gulf in the fall, they drift southward along the coast.

Table 8 gives the average monthly production of brown shrimp for Texas by areas. The monthly variations in catches have already been discussed. The total production declined steadily from the high in August to the April low, but this decline was much less in the two southern areas from October to February. In October the two northern areas produced 67.5 per cent of the brown shrimp taken on the Texas coast. In February, this figure was 20.6 per cent. These facts are clearly shown in Table 9. The trend was reversed in March. It is clear that the brown shrimp population tends to drift southward down the Texas coast during the fall and winter.

TABLE 9

The percentages of the total catch of brown shrimp of the two north and south areas by months, 1956–1959

Areas	October	November	December	January	February
18 and 19	67.5	42.4	35.8	28.2	20.6
19 and 20	32.5	57.6	64.2	71.8	79.4

Unit of Effort and the Catch

In addition to the production statistics from the various areas, the Fish and Wildlife Service workers have collected information by the interview method on days and hours

fished, and the catch, in each of the four Texas areas during the years 1958 and 1959. These data cover 138,716 hours of trawling, which produced 3,974,923 pounds of headed shrimp. This is quite the most extensive data on this subject collected so far on the shrimp fishery.

During the two-year period the boats on which the data were collected caught 28.7 pounds of shrimp per hour. In 1958 the catch was 26.2 pounds per hour; in 1959 it was 29.7 pounds. A comparison made with Table 1 shows that the shrimp catch increased in 1959 above the 1958 catch by 6,013,464 pounds, or 13.6 per cent. The catch per unit of effort increased 3.5 pounds per hour at the same time, or 13.2 per cent. The correspondence is remarkably close. This means that the increased catch in 1959 was due solely to better fishing and not to increased effort by the fishermen.

The tables of data on catch and unit effort by months for each of the four years are quite bulky and will not be presented here. They are on file at the Marine Fisheries Division office of the Game and Fish Commission at Rockport. Table 10 gives the two-

TABLE 10

The monthly average of pounds of heads-off shrimp caught per hour for the years 1958 and 1959 (upper figure), with averages of the total catch for the same period (lower figure), in millions of pounds

January	February	March	April	May	June	July	August	September	October	November	December
16.2	15.4	15.0	11.5	11.0	11.7	45.5	36.5	38.9	38.5	25.9	23.0
.436	.228	.278	.312	.609	1.427	5.456	6.709	7.084	5.912	2.077	1.066

year average catch of shrimp per hour each month for the whole Texas coast, in combination with the total production.

In general, there was strong correspondence between the unit of effort catch and the total catch. During the eight months from November to June, with a low catch of 941,000 pounds a month, the catch per hour of trawling was 16.2 pounds. During the high production months, with an average of 5,757,000 pounds production, the catch per hour of trawling was 39.8 pounds. Though the catch per hour of trawling decreased 60 per cent, the total catch decreased about 85 per cent in the low months as compared to the high months. If these data are typical of the whole fleet, as they are supposed to be, this means that the fishing effort decreases a great deal during the late fall, winter and spring months.

The hourly catch of shrimp in pounds for each month and the total Texas production for the same months are shown graphically in Fig. 6.

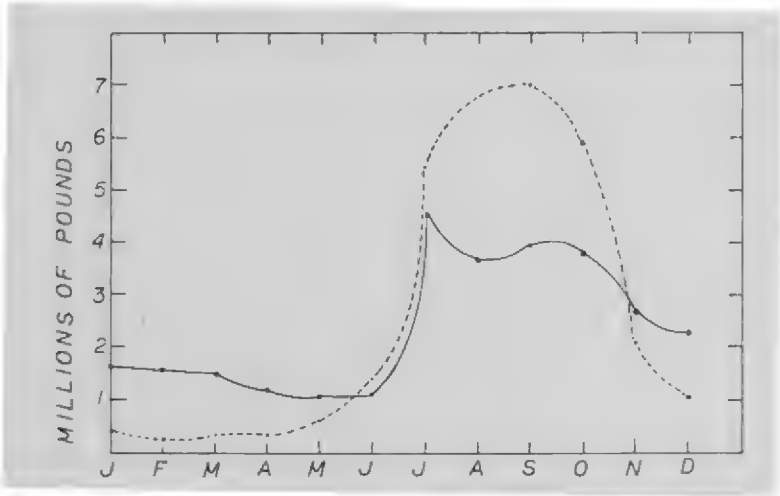

FIG. 6. The catch per hour of shrimp (solid line) compared to the total catch (dotted line) along the Texas Coast. The figures are monthly averages for the years 1958–1959.

Summary

1. The total landings of shrimp tails at United States Gulf Coast ports during the period 1956 to 1959, inclusive, was 426,950,352 pounds. During the same period the total landings of whole shrimp for the South Atlantic and Gulf states was approximately 205,000,000 pounds a year.

2. During the 1956–59 period, Gulf landings of headed shrimp fluctuated between 99 and 115 million pounds with a yearly average of slightly less than 107 million pounds.

3. In terms of per cent of total landings, the rank of the Gulf states for the four-year period was: Texas 41.5, Louisiana 24.7, Florida 23.6, Mississippi 6.5, Alabama 3.8. Of the three top states, the annual fluctuation in per cent was: Louisiana 32.0, Florida 23.6 and Texas 16.7. Texas has the most stable industry. Texas landings varied from 37 to 50 million during the period and averaged 44,295,000 pounds a year.

4. The Gulf landings by species consisted of seabobs (1.2 per cent), white shrimp (20.1), pink shrimp (22.5) and brown shrimp (56.2). Florida led in pink shrimp landings and Louisiana led in white shrimp and seabob landings. Texas led in brown shrimp landings and was second in landings of the other three species.

5. Texas production of heads-off shrimp for the four year period averaged 30,264,927 million pounds annually; 14,030,003 pounds, or 31.7 per cent of the landings, came from out of the state.

6. Texas annual production averaged 26,114,000 pounds of brown shrimp, 4,118,000 pounds of whites, 32,000 pounds of pinks and 359 pounds of seabobs.

7. During the 1930's Texas production of white shrimp averaged 12.3 million pounds of whole shrimp. During the 1940's the comparable figure was 18.3 million pounds. During the 1950's the production was only 6.7 million pounds. The decline in white shrimp production during the past ten years has been over 63 per cent.

8. The Texas coast was divided into four areas, from the Sabine to the Rio Grande. Most of the pink shrimp catch is taken off Corpus Christi Bay. Most white shrimp are taken in the two easternmost areas. The greatest brown shrimp production is from the two middle areas, Freeport south to Aransas Pass.

9. September is the peak month for production of white shrimp. August is the peak month for brown shrimp production. Over 73.0 per cent of the Texas shrimp catch is made during the four months July to October.

10. The total catch of white and brown shrimp declines from the peak months on into the winter, but the percentage decline is less and less southward down the coast. This means that both white and brown shrimp move southward, down the Texas coast during the winter.

11. During the years 1958 and 1959, Texas shrimp boats caught an average of 28.7 pounds of headed shrimp an hour. In general the catch per hour rose and fell with the total production, but the percentage of production fell much greater in the eight low months of the year than the catch per hour.

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Marine Algae From the Gulf Coast of Texas and Mexico

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Abstract

An annotated list of 193 species of marine algae is given as a result of collections made along the coast of the Gulf of Mexico between Rockport, Texas, and the southern part of the State of Vera Cruz, Mexico. One hundred and sixteen of these species were recorded for Texas and 140 for Mexico. The greater number from Mexico is indicative of a richer flora rather than more thorough collecting. South of the Rio Grande, especially along the coast of Vera Cruz and southward, there is an abundance of favorable substrata and warmer inshore water during winter.

The algae listed here represent only a portion of the many collections yet to be studied.

Introduction

Very little is known about the distribution of the marine algae around the shores of the Gulf of Mexico with the exception of the Dry Tortugas area, intensively studied by Taylor (1928). From Everglades, Florida, northward and around the entire Gulf coast to Cuba, our information is spotty and sparse.

[1] Aided by a summer stipend for regional systematics of the western Gulf from the Institute of Marine Science in 1957.

[2] Visiting Research Program, Institute of Marine Science.

Taylor (1935a, 1940, 1941) reported and summarized the records of Texas algae, the present published total of which is now about 60 species.

The east coast of Mexico figured early in marine botanical literature of the New World as a result of collections made in 1845 by Prof. Frederik C. Liebmann of the University of Copenhagen, botanical explorer and describer of many new species of land plants of Mexico. Liebmann sent his collections of algae to J. G. Agardh of Lund, Sweden, who published on them in 1847. In this list of 29 were about 10 species from the State of Vera Cruz and Campeche Banks of the Mexican east coast, the type localities for several of them.

Additional records from the Gulf coast to Mexico were noted by Taylor (1935b, 1941), adding about 45 species to the list, and by Humm (1952, 1956) whose list of 24 from Campeche Banks included 12 not previously reported.

Taylor (1954a, 1954b) summarized the scant knowledge of the algae of the Gulf of Mexico and their known distribution and discussed the nature of the coastline and algal habitats.

Texas Algal Collections

The coast of Texas is a broadly embayed deltaic coastal plain (Price 1954) with about 400 miles of sand beach, many barrier islands and extensive salt and brackish marshes. There are no natural rocks, other than oyster reefs, so that this is one of the principal reasons that the marine algae are limited in abundance. The United States Army Corps of Engineers, however, has constructed five pairs of rubblestone jetties within the past 75 years in order to maintain navigability into the passes of Sabine, Bolivar (Galveston), Freeport, Aransas, and Brazos Santiago. These jetties provide an ideal substratum for algae and thus permit the development of a flora adapted to the other environmental conditions of the area. The Aransas Pass and Brazos Santiago jetties have been the principal source of Texas algae with which this paper is concerned. The three sets of jetties to the north have yet to be studied.

In addition to the jetties, collections were also made in Texas at the following locations: in the southern end of Copano Bay at Rattlesnake Point; along the seawall at Rockport, Aransas Bay; in Redfish Bay, a subdivision of Aransas Bay near the town of Aransas Pass; around Harbor Island in Aransas Bay; at Cline Point near Port Aransas; in the Laguna Madre between Corpus Christi Bay and Port Isabel, especially at channel marker 69, at the Arroyo Colorado cut-off, at flasher 89, in Baffin Bay, Port Mansfield Harbor, and from buoys 119, 129, and 138 near or in the harbor of Port Isabel. The Texas collecting stations listed above are shown on the map in Fig. 1.

The geological nature, hydrography, and other environmental features of the Texas coast have been described in considerable detail by several authors, most of whom have worked at the Institute of Marine Sciences at Port Aransas. Hedgpeth (1948) studied the Laguna Madre of Texas. Collier and Hedgpeth (1950) made a thorough study of the hydrography of the tidal waters of Texas. Additional information and data on the environment are to be found in papers by Whitten *et al.* (1950), Ladd (1951), and Hedgpeth (1953).

The mean tidal range along the Texas coast is usually 1.5 to 2 feet with spring tide extremes of three feet in many places (Aransas Pass and Brazos Santiago jetties, for example).

FIG. 1. The western Gulf of Mexico showing the Texas collecting areas and the principal localities of the Mexican collections.

From 1949 to early 1957, when drought conditions prevailed over south Texas, the average salinity of Copano Bay was above 20 ‰ (Parker 1955). The salinity of Copano Bay is also influenced by the drainage of brine from old oil fields into the Aransas and Mission rivers. All algae collected in Copano Bay in connection with the present work came from water with a salinity of 18 ‰ or above.

In Aransas Bay, the usual annual salinity range of bottom water is between 15 and 25 ‰.

In the Laguna Madre, salinities occasionally become extremely high, sometimes exceeding 100 ‰. These great fluctuations result in mass mortalities of animals and plants, followed by reinvasion when suitable conditions return. During the 1950's, salinities in the Laguna Madre were consistently lower, according to Simmons (1957), than during the period studied by Hedgpeth (1948). Hildebrand and Markey (unpublished manuscript) attribute this to a fortuitous distribution of heavy rainfall on the watershed, and to improved circulation in some areas because of navigational canals.

Water temperatures in Aransas Bay usually exhibit an annual range of from 13 to 30°C. The portion of the Aransas Pass jetty below the low tide level is subjected to a slightly narrower range than this.

Data on salinity, water temperature, light penetration, and other marine environ-

mental factors are of very limited value in understanding the influence of these factors upon the distribution of marine algae unless these data are obtained in direct relationship with the presence of the various species in a given area.

Species of marine algae often appear and disappear in relation to environmental factors other than the annual temperature changes, and they are able to survive short periods of potentially lethal conditions. The actual range of tolerance of the marine algae to fluctuating salinity, temperature, and light intensity is known for a very few, and the interrelations of these and other environmental factors is unknown for macroscopic algae.

Mexican Collections

The collections from Mexico with which this paper is concerned came from three general areas: the Laguna Madre of Mexico along the coast of the state of Tamaulipas at Boca Jesus Maria and Punta Piedras; in the northern part of the state of Vera Cruz in Laguna de Tamiahua and at Cabo Rojo; and from the environs of the city of Vera Cruz in the southern part of the State, southward about 15 miles to the town of Anton Lizardo and the nearby reefs (Blanca and Giote). The majority of the Mexican records listed came from within a three-mile radius of the harbor of Vera Cruz.

Fig. 2 shows the coastal area of Tamaulipas from the Rio Grande to Tampico and the entire Laguna Madre of Mexico. Fig. 3 shows the Punta Piedras area of the Laguna and Boca Jesus Maria pass, the two localities from which collections were obtained.

The outer coast of Tamaulipas is a sandy, high-energy shore like that of Texas and is without rocky outcrops. The Laguna Madre is the largest coastal lagoon in the state. Hildebrand (1958) summarized the available information on the hydrography and fauna of this area. He concluded, on the basis of scanty data, that the entire lagoon was hypersaline throughout the drought years of the 1950's. The northernmost 50 kilometers were classified as a brine pool too salty for fish life, although he noted that this area has passed through several productive and nonproductive cycles since commercial fishing started there in 1911.

No macroscopic algae were observed in the northern sector of the lagoon. All collections came from the Boca Jesus Maria and Punta Piedras localities. Punta Piedras (Point of Rocks) is under the influence of tidal currents and consequent water exchange through Boca Jesus Maria (Eighth Pass) so that the salinity here does not become too high for euryhaline species of marine algae. Local reports indicate that the rainfall is higher here than elsewhere in the Laguna because of the Sierra San Carlos to the westward. Five miles south of Boca Jesus Maria, along the west shore of the barrier island and at Punta Algodon (South Point of Rocks), the salinity was 41 ‰ at the time collections were made on October 22 and 23, 1953. At Punta Piedras on March 19, 1954, salinities of 44 and 46 ‰ were recorded.

Laguna de Tamiahua. The Laguna de Tamiahua (Fig. 4 and 5) is the largest coastal lagoon of the state of Vera Cruz. The main body of water is approximately 60 miles long and has a maximum width of 25 miles. Most of the lagoon, however, is much narrowed and its surface area is further reduced by a number of islands. It is separated from the Gulf of Mexico by a barrier island, Cabo Rojo, which was a peninsula before the construction of the Chijol canal.

DeBuen (1957) has published the only hydrographic description of the area. He occupied 16 stations between December 20 and 23, 1955. The lagoon is apparently

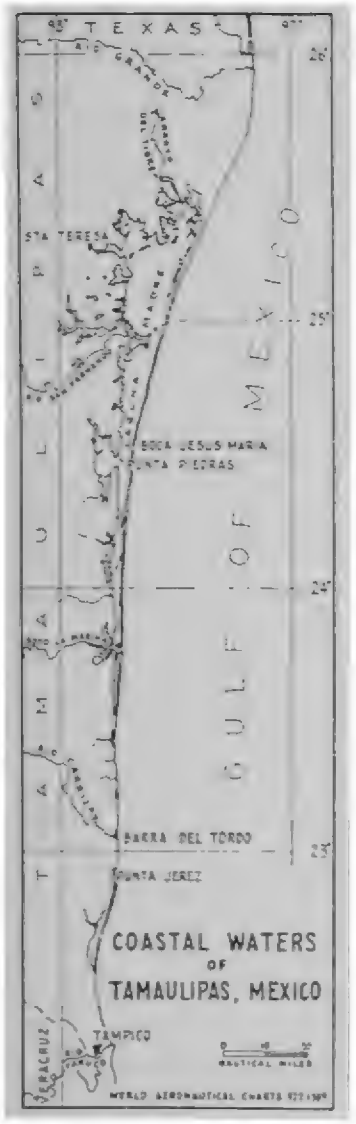

FIG. 2. Collecting stations along the coast of Mexico between the Rio Grande and Tampico.

FIG. 3. Areas from which collections were obtained in the lower Laguna Madre of Mexico near Boca Jesus Maria.

very shallow, and all his station depths are given as less than two meters except for one reported as 3.2 meters west of Isla Juana Ramirez. He found muddy bottom in the deeper central area and muddy sand, sand, or sand mixed with shell along the edges.

DeBuen's salinity determinations were made after one of the most disastrous hurricane seasons ever to strike this portion of the Mexican coast, and about two and a half months after a record flood crest of the Rio Panuco at Tampico on October 5, 1955. In the Laguna north of Isla Toro he recorded salinities of 2.54 to 3.42 ‰.

At the time the algal collections were made, a number of surface salinities were recorded from various parts of the Laguna de Tamiahua in December 1953 and 1954 and in April 1955. These ranged from 4.94 to 12.13 ‰. Additional surface salinity determinations were made for a linear series of 11 stations from the northern entrance of the intracoastal canal to Isla Martinica on April 28–29, 1955. The range was from 18.23 ‰ on the north to 9.75 ‰ at Isla Martinica.

As pointed out by DeBuen, the primary factors which control salinity in the Laguna are rainfall and runoff, since connections to the sea are tenuous. In this region there are pronounced rainy and dry seasons. The rainy season normally occurs from the end of June to the end of October, although there is considerable yearly variation. During the rainy season the level of the Laguna may rise more than a meter and remain high for days. DeBuen (1957) reports a rise of 1.30 meters during the 1955 hurricane.

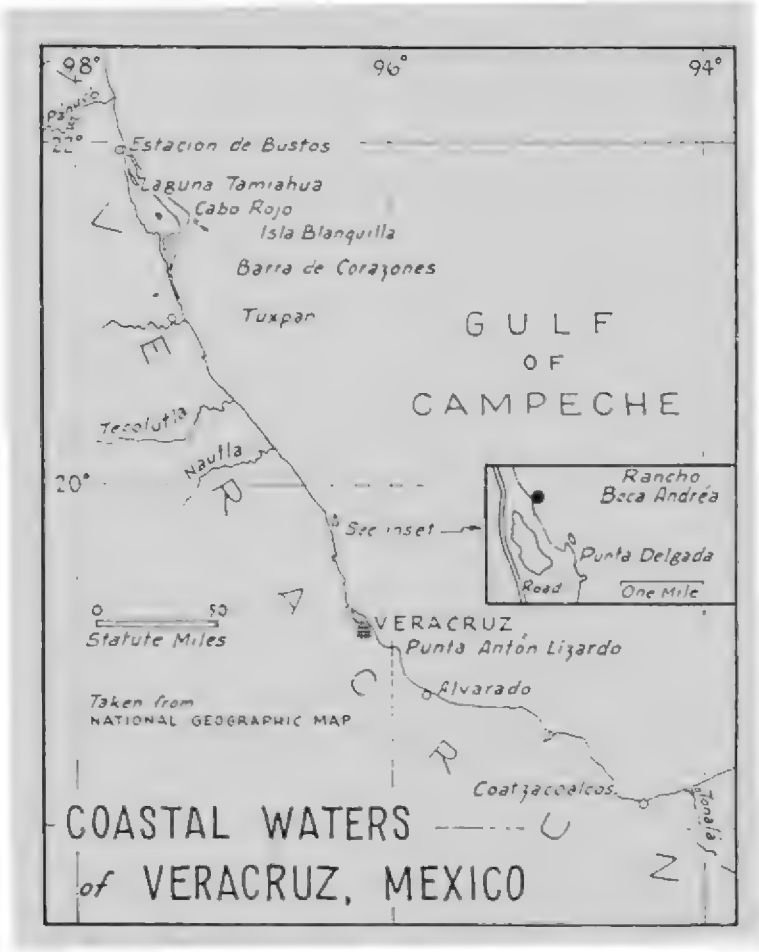

FIG. 4. Collecting localities of the southwestern Gulf of Mexico along the coast of Vera Cruz.

FIG. 5. Collecting areas of the upper Laguna de Tamiahua, Vera Cruz, Mexico.

In some years the northern part of the lagoon may become hypersaline when the rainy season is unduly delayed, however, the normal salinities are well below oceanic values even during the dry season and are sometimes only slightly brackish during rainy season floods.

DeBuen (1957) reported surface water temperatures of 20.8 to 22.9°C for December 20–23, 1955. The highest water temperature recorded, 29°C, was in Estero Cucharas on July 13, 1956.

Blanquilla Reef. The most northerly coral formation in shallow water of the western Gulf of Mexico is Blanquilla Reef (Isla Blanquilla) located about three miles southeast of Cabo Rojo (Fig. 4). Moore (1958) has studied the reef and considers it a transitional area between subtropical and tropical marine habitats. The reef is about 800 yards long, 500 yards wide, with its axis north-south. The eastern or windward side slopes gradually and faces the open Gulf where it is subject to strong wave action. The dead corals here are coated with rose-pink encrusting coralline algae. The westward side of the reef ends in a small cliff about 10 feet high and the depth of the water between the reef and Cabo Rojo reaches 85 feet. The salinity of the water surrounding the reef is essentially that of the open Gulf.

Rancho Boca Andrea. About 50 miles north of the city of Vera Cruz and adjacent to Punta Delgada (North) is Rancho Boca Andrea where the substratum is part of the Jalapa volcanic salient (Price, 1954). This is a strictly marine environment noteworthy

for the variety of marine invertebrate animals present. The algal collections were obtained from the base of a lava cliff about 200 feet high where there were many large boulders.

Vera Cruz Harbor Area. The southeast breakwater of Vera Cruz harbor, Los Hornos reef, Punta Hornos, a rock breakwater at Balneario Villa del Mar provided collections of algae from the immediate Vera Cruz area and are shown in the insert of Fig. 6. Other collecting stations shown in Fig. 6 include Isla Sacrificios, about two miles southeast of

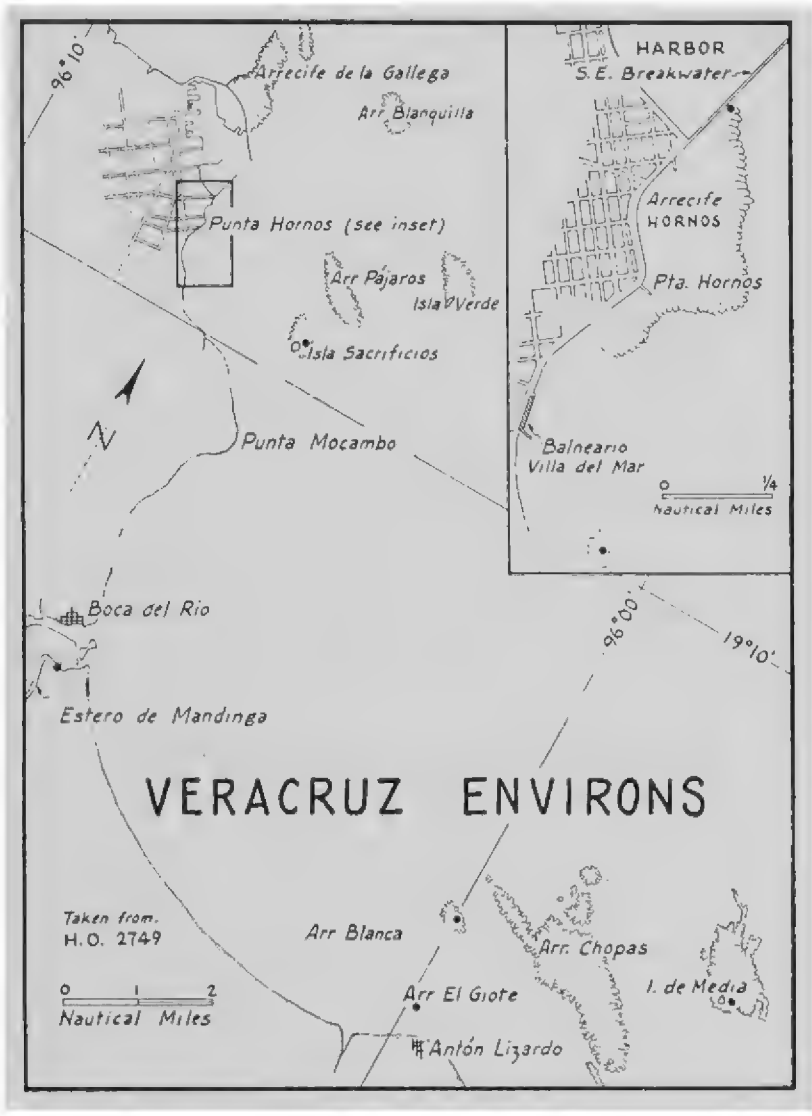

FIG. 6. A detailed map of the area from the city of Vera Cruz to Anton Lizardo with an inset to show Los Hornos reef and breakwater and the location of Balneario Villa del Mar.

Vera Cruz; a sea wall and an old reef just north of Boca del Rio; and the Estero de Mandinga just south of Boca del Rio. All these stations are strictly marine habitats with rocky substrate and a wide variety of algae with the exception of Estero de Mandinga where the water is brackish.

Los Hornos is an old fringing reef on the south side of the entrance to Vera Cruz harbor with the southeast breakwater running along its northern edge. Los Hornos is actually a double reef in that there is an inner and outer reef linear in shape and parallel so that they have the appearance of breakwaters. Old coral boulders stand above the high tide line, but all rock surfaces are wetted frequently by surf. Los Hornos inner reef is characterized by the absence of heavy surf whereas the outer reef is subject to strong wave action, especially during the winter. Although there is a little live coral on the outer reef, none was seen on the inner reef. The two reefs are separated by deeper water which serves as a channel leading into the Escuela Nautica Fernando Siliceo. There are

extensive sea grass beds between the reef and the shore, mostly of *Thalassia testudinum* König but in some areas *Diplanthera wrightii* (Ascherson) Ascherson is predominant.

Anton Lizardo. Two reefs, Arrecife Blanca and Arrecife El Giote, just north of Anton Lizardo and about 10 miles south of the city of Vera Cruz proved to be good collecting areas. They are shown in Fig. 6. Around Blanca reef are extensive areas of calcareous sands providing a suitable habitat for *Siphonales*, especially the genus *Caulerpa*.

Annotated List of Species

Cyanophyta

Order Chroccoccales

Family Chroccoccaceae

Agmenellum thermale (Kützing) Drouet and Daily

Texas: Aransas Bay 1 mile east of the town of Aransas Pass on *Diplanthera wrightii* (Ascherson) Ascherson.

Kützing 1843, p. 163 (as *Merismopedia thermalis*); Drouet and Daily 1956, p. 89, Fig. 140; Humm and Darnell 1959, p. 270.

Anacystis aeruginosa (Zanardini) Drouet and Daily

Texas: Aransas Bay 1 mile east of the town of Aransas Pass on *Diplanthera wrightii.*

Zanardini 1862–76, Vol. XVII, p. 162 (1872), (as *Palmogloea aeruginosa*); Drouet and Daily 1956, p. 76, Fig. 110; Humm and Caylor 1957, p. 232, pl. I, Fig. 1.

Anacystis dimidiata Drouet and Daily

Texas: From scrapings of a piling, channel marker 21, Laguna Madre channel. On *Diplanthera wrightii* from shallow water in Aransas Bay about 1 mile east of the town of Aransas Pass.

Drouet and Daily 1956, p. 70, Fig. 105; Humm and Caylor 1957, p. 232, pl. I, Fig. 2–3.

Coccochloris elabens Drouet and Daily

Texas: At the base of a clump of *Acetabularia crenulata* from shallow water near flasher 49, Laguna Madre channel, between Ports Isabel and Mansfield.

Drouet and Daily 1956, p. 28, Fig. 168; Tilden 1910, p. 35, pl. II, Fig. 19 (as *Microcystis elabens* (Meneghini) Kützing).

Family Chamaesiphonaceae

Entophysalis conferta Drouet and Daily

Texas and Mexico: Widely distributed and very common; probably could be recorded from all stations from which collections have been made.

Drouet and Daily 1956, p. 111, Fig. 211; Humm and Caylor 1957, p. 234, pl. I, Fig. 6–7.

Entophysalis deusta Drouet and Daily

Texas and Mexico: In shells of molluscs and other forms of limestone, probably at all stations; on top surface of west jetty of Aransas Pass mixed with *Calothrix crustacea.*

Drouet and Daily 1956, p. 103, Fig. 191; Humm and Caylor 1957, p. 234, pl. I, Fig. 4–5.

ORDER OSCILLATORIALES
FAMILY OSCILLATORIACEAE

Spirulina subsalsa Oersted

Texas: On *Diplanthera wrightii* from shallow water near marker 21, Laguna Madre channel, and on *Laurencia poitei* near flasher 89 near the Port Isabel end of the Laguna Madre.

Mexico: On shells (dead) from *Thalassia testudinum* flats, lee side of inner Los Hornos reef, Vera Cruz.

Oersted 1842, p. 566, pl. VII, Fig. 4; Gomont 1892, p. 253, pl. 7, Fig. 32; Humm and Caylor 1957, p. 235, pl. I, Fig. 11; Humm and Darnell 1959, p. 270.

Oscillatoria corallinae (Kützing) Gomont

Texas: Forming large brown patches or a very fragile sheet over *Thalassia testudinum* in shallow water, Aransas Bay about 1 mile east of the town of Aransas Pass; on *Spyridia aculeata*, west jetty at Port Aransas; on *Chondria curvilineata* from buoy 129 in the harbor of Port Isabel.

Gomont 1892, p. 218, pl. 6, Fig. 21; Tilden 1910, p. 70, pl. IV, Fig. 16.

Oscillatoria laetevirens Crouan

Texas: On buoy 128 in the harbor of Port Isabel.

Crouan 1860, p. 371; Gomont 1892, p. 226, pl. 7, Fig. 11.

Oscillatoria nigro-viridis (Thwaites) Gomont

Texas: In the intertidal zone on bridge supports of the causeway between Port Isabel and Padre Island. Mexico: On oysters in the intertidal zone of a bar at a creek mouth, Laguna Madre of Mexico.

Gomont 1892, p. 217, pl. 6, Fig. 20; Tilden 1910, p. 69, pl. IV, Fig. 12; Fremy 1938, p. 32; Humm and Caylor 1957, p. 234, pl. I, Fig. 8.

Oscillatoria salinarum Collins

Mexico: On oysters in the intertidal zone of a bar at a creek mouth, Laguna Madre of Mexico.

Collins 1906, p. 105; Tilden 1910, p. 77.

Phormidium subuliforme Gomont

Texas: On the supports of flasher 89, Laguna Madre channel at Port Isabel.

Gomont 1892, p. 169, pl. 4, Fig. 26; Tilden 1910, p. 99, pl. IV, Fig. 67.

Lyngbya confervoides Gomont

Texas: On rocks in the intertidal zone, Boca Chica jetty, Cameron County.

C. Agardh 1824, p. 73; Gomont 1892, p. 136, pl. 3, Fig. 5–6; Fremy 1938, p. 29; Humm and Caylor 1957, p. 235, pl. II, Fig. 1.

Lyngbya gracilis (Meneghini) Rabenhorst

Texas: On *Hypnea musiciformis* from shallow water between the causeway and ship channel, Port Isabel.

Rabenhorst 1865, p. 145; Gomont 1892; p. 124, pl. 2, Fig. 20; Tilden 1910, p. 117, pl. V, Fig. 36; Fremy 1938; p. 25; Humm and Darnell 1959, p. 270.

Lyngbya lutea (C. Agardh) Gomont

Texas: On bridge supports in the intertidal zone, causeway between Port Isabel and Padre Island.

Gomont 1892, p. 141, pl. 3, Fig. 12–13; Tilden 1910, p. 114, pl. V, Fig. 30–31; Fremy 1938, p. 30; Humm and Caylor 1957, p. 235, pl. II, Fig. 2.

Lyngbya majuscula Gomont

Mexico: On oysters in the intertidal zone, Laguna Madre.

Gomont 1892, p. 131, pl. 3, Fig. 3–4; Tilden 1910, p. 123, pl. V, Fig. 42; Taylor 1928, p. 44, pl. 1, Fig. 19; Fremy 1938, p. 28; Humm and Darnell 1959, p. 270.

Symploca atlantica Gomont

Texas: On bridge supports, causeway between Port Isabel and Padre Island.

Gomont 1892, p. 109, pl. 2, Fig. 5; Tilden 1910, p. 129, pl. V, Fig. 48; Humm and Caylor 1957, p. 238, pl. II, Fig. 11.

Symploca hydnoides Gomont

Texas: A large drifting mass in the Laguna Madre channel near flasher 49 between Port Isabel and Port Mansfield; in slash pools above the high tide line, Boca Chica jetty, Brazos Santiago, Cameron County; on buoy 325, Laguna Madre channel. Mexico: On the lee side of Los Hornos reef, Vera Cruz. Widely distributed in the area.

Gomont 1892, p. 106, pl. 2, Fig. 1–4; Tilden 1910, p. 129, pl. V, Fig. 49; Fremy 1938, p. 22.

Microcoleus chthonoplastes Thuret

Texas: On *Thalassia* flat about 1 mile east of the town of Aransas Pass in Aransas Bay, entangled within a clump of loose *Cladophora gracilis*. Mexico: On mud surface of an oyster bar, Laguna Madre.

Thuret 1875, p. 378; Gomont 1892, p. 353, pl. 14, Fig. 5–8; Fremy 1938, p. 16; Humm and Caylor 1957, p. 238, pl. II, Fig. 10.

Skujaella erythraea (Ehrenberg) J. deToni

Texas: On other algae from the causeway bridge supports, and on algae from a buoy in the harbor, Port Isabel. Probably this material became mechanically and temporarily attached to objects in the Port Isabel harbor from a heavy population occurring as plankton in the surrounding water. This is the genus responsible for the color and name of the Red Sea.

There can be no question about its occurrence, at least periodically, along the Mexican coast.

Ehrenberg 1830, p. 506; Gomont 1892, p. 196, pl. V, Fig. 27–30; Tilden 1910, p. 84, pl. IV, Fig. 40 (as *Trichodesmium erythraeum* Ehrenberg).

Family Nostocaceae

Nodularia harveyana (Thwaites) Thuret

Mexico: On Thalassia in shallow water, Punta Hornos, Vera Cruz.

Thuret 1875, p. 378; Bornet and Flahault 1888, p. 243; Humm and Caylor 1957, p. 240, pl. II, Fig. 1.

Family Scytonemataceae

Plectonema terebrans Bornet and Flahault

Texas. On oyster shell from causeway bridge supports between Port Isabel and Padre Island.

Bornet and Flahault 1889, p. 163, pl. 10, Fig. 5–6; Gomont 1892, p. 102; Tilden 1910, p. 209, pl. XI, Fig. 6.

Family Stigonemaceae

Mastigocoleus testarum Lagerheim

Mexico: In old shells, Blanca reef, Anton Lizardo, Vera Cruz. Probably at all stations where collections have been made but overlooked unless old shells are decalcified. It is surely present along the Texas coast.

Lagerheim 1886, p. 65, pl. 1; Bornet and Flahault 1887, p. 54; Tilden 1910, p. 237. pl. XIV, Fig. 12; Humm and Caylor 1957, p. 240, pl. III, Fig. 3.

Family Rivulariaceae

Calothrix crustacea Thuret

Texas: On upper surface of west jetty where wet occasionally by sea spray, Port Aransas; on *Penicillus capitatus*, flats between causeway bridge and ship channel, Port Isabel. Mexico: Intertidal zone of oyster bar, Laguna Madre.

On the Aransas Pass jetty, this species withstands desiccation, exceptionally high temperatures at midday during the summer when there is no splash, fresh water during rains and it is walked upon almost daily by sports fishermen. During dry weather, crystals of sea salt form upon the patches of plants.

Thuret in Bornet and Thuret 1876–80, p. 13, pl. 4; Bornet and Flahault 1886, p. 359; Tilden 1910, p. 264, pl. XVII, Fig. 2–6; Fremy 1938, p. 35; Fan 1956, p. 172.

Chlorophyta

Order Ulotrichales

Family Chaetophoraceae

Entocladia viridis Reinke

Texas: On *Agardhiella tenera*, west jetty of Aransas Pass. Mexico: In test of hydroids from an old reef along shore about one mile north of Boca del Rio, Vera Cruz; on *Gracilaria foliifera*, Los Hornos reef, Vera Cruz. Widely distributed as an epiphyte along the entire Gulf coast.

Reinke 1879, p. 476, pl. VI; Taylor 1957, p. 54, pl. 2, Fig. 1–2; Humm and Caylor 1957, p. 242, pl. IV, Fig. 6.

Entocladia wittrockii Wille

Texas: On *Polysiphonia ramentacea*, Rattlesnake Point, Copano Bay. While *E. viridis* is apparently continuous along the Atlantic coast from New England to Florida and around the Gulf of Mexico, *E. wittrockii* is known only from Maine to Connecticut, except for a report in the Gulf of Mexico by Phillips and Springer (1960).

It seems unlikely that the same species occurs in two such widely-separated habitats though one so inconspicuous could easily have been overlooked in the intermediate areas. Because of its microscopic and epiphytic or endophytic nature and the variations in cell size and shape. it presents taxonomic difficulties. Kylin (1938, p. 72; 1949, p. 37) regards this species as *Ectochaete wittrockii* (Wille) Kylin as he found small hyaline hairs arising from some of the cells. These evidently have not been found in New England material and seemed to be absent from the Texas material.

Wille 1880, p. 3, pl. I, Fig. 1–7; Collins 1909, p. 139, Fig. 100; Taylor 1957, p. 54.

Ulvella lens Crouan

Texas: On *Dictyota dichotoma*, west jetty of Aransas Pass; on *Thalassia* in Aransas

Bay about 1 mile east of the town of Aransas Pass. Mexico: On hydroids from an old reef along shore and about 1 mile north of Boca del Rio, Vera Cruz.

Probably continuous around the Gulf coast but easily overlooked because of its microscopic size. Comments concerning the apparent confusion of two entities under this name are given by Humm and Caylor 1957.

Crouan 1859, p. 288, pl. XXII, Fig. E. Nos. 25–27; Børgesen 1913, Part 1, p. 11; Newton 1931, p. 64; Humm and Darnell 1959, p. 270.

Phaeophila dendroides (Crouan) Batters

Texas: On *Polysiphonia ramentacea* from Rattlesnake Point, Copano Bay; on *Thalassia* in Aransas Bay, 1 mile east of the town of Aransas Pass.

Like *Entocladia viridis* and *Ulvella lens*, this species is probably continuous around the Gulf coast, but is often overlooked because it is microscopic and usually epiphytic. It was recorded from Campeche Banks by Humm (1952) as *P. floridearum*.

Crouan 1867, p. 128, pl. 8, Fig. 59 (as *Ochlochaete dendroides*); Taylor 1928, p. 58, pl. 3, Figs. 4–6 (as *P. floridearum* Hauck); Humm and Caylor 1957, p. 242, pl. V, Fig. 1 (as *P. floridearum*); Humm and Darnell 1959, p. 270; Humm and Taylor 1961, Fig. 3G, H.

Family Chaetopeltidaceae

Diplochaete solitaria Collins

Mexico: On *Gracilaria foliifera*, Punta Hornos, Vera Cruz. This species is much more widely distributed than records indicate. It is easily overlooked because it is microscopic and single-celled and because of its superficial resemblance to a diatom.

Collins 1901, p. 242; 1909, p. 198, Fig. 99; Taylor 1957, p. 59; 1960, p. 53.

Order Ulvales

Family Ulvaceae

Enteromorpha clathrata (Roth) Greville

Texas: Intertidal zone, west jetty, Aransas Pass; along the channel through the Laguna Madre at many stations between Corpus Christi Bay and Port Isabel. Mexico: on *Thalassia*, inner Los Hornos reef, lee side, Vera Cruz (variety *crinita*).

The material from Mexico would previously have been referred to *E. crinita* (Roth) J. Agardh, but it seems better to regard it as a form of *E. clathrata* as suggested by Taylor 1957, p. 64.

Greville 1830, p. 181; Collins 1909, p. 199; Børgesen 1913, p. 7; Taylor 1954a, p. 93; Humm and Darnell 1959, p. 271; Humm and Taylor 1961, Fig. 6A; Taylor 1960, p. 58.

Enteromorpha flexuosa (Wulfen) J. Agardh

Texas: Common along the waterfront at Rockport; on a retaining wall and boulders in the Laguna Madre at Port Isabel; many other stations. Mexico: Reef at Villa del Mar Balneario, Los Hornos inner reef and jetty, Vera Cruz and elsewhere.

J. G. Agardh 1882, p. 126; Vickers 1908, p. 15, pl. III; Taylor 1960, p. 61; Humm and Taylor 1961, Fig. 6 C.

Enteromorpha lingulata J. Agardh

Texas: Port Aransas, Rockport, Port Mansfield, Port Isabel, Laguna Madre and

other stations. Mexico: On *Thalassia* at Punta Hornos, Vera Cruz. A species that is sometimes difficult to distinguish from *E. flexuosa.*

Probably continuous around the entire Gulf coast.

J. G. Agardh 1882, p. 143; Taylor 1942, p. 13; Børgesen 1913, p. 7; Blomquist and Humm 1946, p. 4; Humm and Taylor 1961.

Enteromorpha prolifera (O. F. Müller) J. Agardh

Mexico: On Thalassia between the reef and the beach at Villa del Mar Balneario, Vera Cruz.

J. G. Agardh 1882, p. 129, pl. IV, Fig. 103–4; Taylor 1928, p. 56, pl. 3, Fig. 19; Humm and Taylor 1961, Fig. 6B.

Enteromorpha salina Kützing

Mexico: Common on leaves of *Thalassia* in 2–3 feet of water at Punta Hornos and between the reef and the beach at Villa del Mar Balneario, Vera Cruz.

Kützing 1845, p. 248; 1856, p. 13, pl. XXXVI, Fig. 2; Collins 1909, p. 122; Taylor 1928, p. 56; 1960, p. 56.

Ulva lactuca Linnaeus

Texas: Common or abundant at most stations from which collections were made. Mexico: Widely distributed, especially var. *rigida* (C. Agardh) LeJolis.

Collins 1909, p. 134; Taylor 1928, p. 57, pl. 3, Fig. 20–21 and pl. 7, Fig. 7; 1960, p. 65.

Ulva fasciata Delile

Texas: Associated with *Centroceras clavulatum* to form the uppermost stratum of macroscopic algae along the jetties of Aransas Pass, and the jetties at Brazos Santiago, Cameron County. Mexico: Los Hornos reef, near Boca del Rio and on *Thalassia* between the reef and beach at Villa del Mar, Vera Cruz.

Delile 1813, p. 153, pl. LVIII, Fig. 5; Vickers 1908, p. 15, pl. II; Taylor 1960, p. 66, pl. 1, Fig. 4; Humm and Taylor 1961, Fig. 17.

Order Cladophorales
Family Cladophoraceae

Chaetomorpha brachygona Harvey

Texas: Near Cline Point, Port Aransas, a loose mass in shallow water. Mexico: Among *Thalassia*, lee side of Los Hornos inner reef, Vera Cruz.

Harvey 1858, p. 87, pl. XLVI, Fig. A; Collins 1909, p. 245; Taylor 1928, p. 60, pl. 4, Fig. 12; 1960, p. 70, pl. 2, Fig. 9.

Chaetomorpha gracilis Kützing

Texas: Aransas Bay about one mile east of the town of Aransas Pass, entangled in a clump of loose *Cladophora gracilis* in shallow water among *Thalassia.*

Kützing 1845, p. 203; Børgesen 1913, p. 19; Taylor 1928, p. 60, pl. 4, Fig. 13; 1960, p. 70.

Chaetomorpha media (C. Agardh) Kützing

Mexico: On rocks in the surf (short, dense tufts about one inch tall), Los Hornos reef; reef at the edge of Villa del Mar Balneario; old reef along the shore about one mile north of Boca del Rio; all localities in Vera Cruz.

Kützing 1849, p. 380; Vickers 1908, p. 17, pl. VIII (as *C. antennina* Kützing); Taylor 1942, p. 22; 1960, p. 73.

Rhizoclonium riparium (Roth) Harvey

Texas: On shells near a creek mouth, Laguna Madre near Port Mansfield. Mexico: On shells from *Thalassia* flats, inner Los Hornos reef on the lee side, Vera Cruz; on an intertidal oyster bar at a creek mouth, Laguna Madre of Mexico.

Harvey 1846–51, Synop. 314, pl. CCXXXVIII; Collins 1909, p. 247; Humm and Taylor 1961, Fig. 5J.

Cladophora catenata (C. Agardh) Ardissone

Mexico: Growing within a clump of *Amphiroa fragilissima* from the breakwater at the north end of the Los Hornos reef, Vera Cruz.

Collins (1909) indicates Jamaica for this species, probably on the basis of an herbarium specimen, as he does not list it in Algae of Jamaica (1901), nor is it listed by Murrary in Catalogue of the marine algae of the West Indian region (1889).

Rabenhorst 1863, No. 1293 (Algen, by F. Ardissone); Hamel 1924a, p. 293, pl. V; Taylor 1960, p. 83.

Cladophora delicatula Montagne

Texas: Boca Chica jetty and on *Diplanthera,* Padre Island jetty, Brazos Santiago, Cameron County. Mexico: On *Diplanthera* near creek mouth, Boca Jesus Maria and from an oyster bar near a creek mouth, Laguna Madre of Mexico.

Montagne 1850, p. 302; Collins 1909, p. 257; Humm and Darnell 1959, p. 271; Taylor 1960, p. 87.

Cladophora fascicularis (Mertens) Kützing

Texas: Forming a dense, green fringe high in the intertidal zone on rocks and the sea wall at Rockport; on buoy 129 in Port Isabel harbor and buoy 119 in the Laguna Madre channel just north of Port Isabel. Mexico: On *Thalassia* between the reef and the beach and on the reef at the south edge of Villa del Mar Balneario; on an old reef along shore about one mile north of Boca del Rio, Vera Cruz.

Kützing 1843, p. 268; Vickers 1908, p. 18, pl. XIII; Collins 1909, p. 265; Humm and Taylor 1961, Fig. 6F; Taylor 1960, p. 91, pl. 3, Fig. 3.

Cladophora flexuosa (Griffiths) Harvey

Mexico: *Thalassia* flats, inner Los Hornos reef, Vera Cruz.

Harvey 1846–51, pl. CCCLIII; Collins 1909, p. 259; Hoyt 1917–18, p. 428; Taylor 1960, p. 89.

Cladophora glaucescens (Griffiths) Harvey

Texas: On shells in about four feet of water just east of channel marker 69, Laguna Madre; on stranded loggerhead turtle, Port Aransas. Mexico: On *Thalassia* at Punta Hornos, Vera Cruz.

Harvey 1846–51, Synop. 308, pl. CXCVI; Collins 1909, p. 256; Humm and Taylor 1961.

Cladophora gracilis (Griffiths) Kützing

Texas and Mexico: Common in the Laguna Madre of both Texas and Mexico and at many stations. Probably continuous around the Gulf coast.

Kützing 1845, p. 215; Harvey 1846–51, pl. XVIII; Collins 1909, p. 262; Taylor 1960, p. 90; Humm and Taylor 1961, Fig. 5 A-B.

Cladophora repens (J. Agardh) Harvey

Texas: In Baffin Bay in about 2½ feet of water at Riviera Beach.

Harvey 1846–51, pl. CCXXXVI; Collins 1918, p. 83; Taylor 1928, p. 64, pl. 4, 6, and 7; 1960, p. 82.

Family Gomontiaceae

Gomontia polyrhiza (Lagerheim) Bornet and Flahault

Mexico: In old shells, Blanca reef, Anton Lizardo, Vera Cruz. Probably continuous around the Gulf of Mexico but overlooked unless old shells are decalcified, as it bores into various forms of limestone.

Bornet and Flahault 1888, p. 163; 1889, p. CLII, pl. VI–VIII; Collins 1909, p. 290, Fig. 135; Taylor 1928, p. 58, pl. 3, Fig. 11; 1960, p. 53; Humm and Taylor 1961, Fig. 9 E.

Order Siphonales

Family Bryopsidaceae

Bryopsis pennata Lamouroux

Texas: On bridge supports of the causeway between Port Isabel and Padre Island mixed with *Centroceras calvulatum*; on vertical rock surfaces below low tide, Port Aransas jetty, where it was abundant and one of the lowest of the algae on the rocks.

Lamouroux 1809a, p. 134, pl. 3, Fig. 1; Vickers 1908, p. 30, pl. LII; Collins 1909, p. 325; Humm and Taylor, 1961, Fig 7 H-I.

Bryopsis hypnoides Lamouroux

Texas: Abundant below low tide on the jetty at Port Aransas. Mexico: On *Thalassia* from inner Los Hornos reef, lee side, Vera Cruz.

Lamouroux 1809a, p. 135, pl. I, Fig. 2–2b; Vickers 1908, p. 30, pl. LIII; Collins 1909, p. 323; Blomquist and Humm 1946, p. 5; Taylor 1960, p. 130.

Family Codiaceae

Halimeda opuntia (Linnaeus) Lamouroux

Mexico: Los Hornos reef and at the southwest corner of Isla Sacrificios, Vera Cruz.

Lamouroux 1812, p. 186; Vickers 1908, p. 25, pl. XXXV; Taylor 1960, p. 176, pl. 23, Fig. 3; pl. 24, Fig. 1; Hillis 1959, p. 359, pl. 2, Fig. 7–8; pl. 5, Fig. 3–4; pl. 6, Fig. 6; pl. 7, Fig. 3, pl. 10.

Halimeda tuna (Ellis and Solander) Lamouroux

Mexico: At the southwest side of Isla Sacrificios, Vera Cruz.

Lamouroux 1812, p. 186; Vickers 1908, p. 24, pl. XXXIII; Collins 1909, p. 320; Rayss 1955, p. 30, Fig. 4; Hillis 1959, p. 342, pl. 1, Fig. 4–5, pl. 5, Fig. 9; pl. 6, Fig. 7; pl. 20, Fig. e; Taylor 1960 p. 178, pl. 24, Fig. 5.

Penicillus capitatus Lamarck

Texas: On muddy-sand flats in 3–5 feet of water between the causeway bridge and ship channel, Port Isabel. In some areas there were several hundred plants per square meter.

Lamarck 1813, p. 299; J. Agardh 1886, p. 62; Collins 1909, p. 312; Taylor 1960, p. 171, pl. 21, Fig. 2; pl. 25, Fig. 4.

Rhipocephalus phoenix (Ellis and Solander) Kützing

Mexico: Blanquilla reef, Cabo Rojo, and at the southwest side of Isla Sacrificios, Vera Cruz.

Kützing 1849, p. 506; Harvey 1858, p. 46, pl. XLIII; J. Agardh 1886, p. 65; Collins 1909, p. 313, fig. 150; Taylor 1960, p. 174, pl. 22, Fig. 2.

Codium isthmocladum Vickers

Mexico: Los Hornos reef and jetty, Vera Cruz.

Vickers 1905, p. 57; 1908, p. 23, pl. XXVIII; Silva 1960, p. 503, pl. 110, pl. 111, Fig. a–b; pl. 115, 116; Taylor 1960, p. 186, pl. 26, Fig. 3.

Codium taylori Silva

Mexico: Common on the lee side of Los Hornos reef, Vera Cruz.

Silva 1960, p. 510, pl. 112, 118b, 119, 120a, b; Taylor 1960, p. 188, pl. 26, Fig. 1; Humm and Taylor 1961, Fig. 7 B, 12 D.

Family Caulerpaceae

Caulerpa mexicana (Sonder) J. Agardh

Texas: In shallow water between the causeway bridge and ship channel, Port Isabel. A small, inconspicuous form.

Kützing 1849, p. 496; Harvey 1858, p. 16, pl. XXXVII A; J. G. Agardh 1872, p. 13 (as *C. crassifolia* (C. Agardh) J. Agardh); Weber-van Bosse 1898, p. 289 (as *C. pinnata* Weber-van Bosse); Collins 1909, p. 333 (as *C. crassifolia*); Taylor 1960, p. 141, pl. 12, Fig. 2–5; Humm and Taylor 1961, Fig. 9 H, 10 D.

Caulerpa cupressoides (West) C. Agardh

Mexico: At the south end of Los Hornos reef jetty and on the fringing reef off the southwest side of Isla Sacrificios, Vera Cruz. The latter var. *disticha* Weber-van Bosse.

C. A. Agardh 1822, p. 441; Harvey 1858, p. 21, pl. XXXIX; J. G. Agardh 1872, p. 23; Weber-van Bosse 1898, p. 323, pl. XXVII and XXVIII; Taylor 1928, p. 96, pl. 12, Fig. 10–11, 21; pl. 13, Fig. 1; 1960, p. 146, pl. 14, Fig. 3–4, 6; pl. 15, Fig. 1–4, pl. 18, Fig. 11–13; Humm and Taylor 1961, Fig. 12.

Caulerpa racemosa (Forsskal) J. Agardh

Mexico: Los Hornos reef and the break water at the north end of the reef (var. *uvifera* (Turner) J. Agardh); Blanquilla reef at Cabo Rojo, Vera Cruz (a peculiar dwarf form).

J. G. Agardh 1872, p. 35; Weber-Van Bosse 1898, p. 357, pl. XXXI, Fig. 5–8, pl. XXXII, Fig. 1–7, pl. XXXIII; Taylor 1928, p. 101, pl. 12, Fig. 3–5, 6, 8, 14, pl. 13, Fig. 3, 8, 9–11; 1960, p. 151, pl. 17, Fig. 1, 3, 4, 6, 7; pl. 18, Figs. 2–5, 7.

Caulerpa sertularioides (Gmelin) Howe

Texas: Port Isabel in 3–5 feet of water between causeway bridge and ship channel.

Mexico: Vera Cruz at Los Hornos reef, at the south end of Isla Sacrificios, near Boca del Rio, at Giote reef and at Blanca reef, Anton Lizardo (forma *farlowi* (Weber) Børgesen and forma *brevipes* (J. Agardh) Svedelius).

Howe 1905, p. 576; Vickers 1908, p. 26, pl. XLII; Weber-van Bosse 1898, p. 294, pl. XXIV, Fig. 4–6 (as *C. plumaris* C. Agardh); Taylor 1928, p. 103, pl. 12, Fig. 2, 16–1, pl. 13, Fig. 5; 1960, p. 144, pl. 13, Fig. 1–7; Humm and Taylor 1961, Fig. 9 F.

Caulerpa vickersiae Børgesen

Mexico: Los Hornos reef, Vera Cruz, on the breakwater at the north end and on the surfside of the reef. Scattered sparingly among tufts of *Amphiroa fragilissima* but generally abundant. This is a small, inconspicuous species that grows in exposed places entangled among corallines or at the base of soft corals.

Børgesen 1912, p. 129, Fig. 2; Taylor 1928, p. 104, pl. 12, Fig. 20, pl. 13, Fig. 12; 1932, p. 396, pl. XXXVI; 1960, p. 137, pl. 10, Fig. 3–9.

Family Phyllosiphonaceae

Ostreobium quekettii Bornet and Flahault

Texas: In oyster shells on bridge supports, causeway between Port Isabel and Padre Island. Probably continuous around the Gulf coast but rarely reported because of its habit of penetrating limestone.

Bornet and Flahault 1889, p. CLXI, pl. IX, Fig. 5–8; Collins 1909, p. 328, Fig. 159; Humm and Taylor 1961, Fig. 3F, 9G.

Order Dasycladales

Family Dasycladaceae

Acetabularia crenulata Lamouroux

Texas: Common along the Laguna Madre channel on old shells and to some extent on buoys; in Aransas Bay.

Lamouroux 1816, p. 249, pl. 8, Fig. 1; Solms-Laubach 1895, p. 24, pl. I, Fig. 1–3: Vickers 1908, p. 29, pl. XLVIII; Collins 1909, p. 378; Taylor 1928, p. 67, pl. 5, Fig. 11, 22–24 (as *Acetabulum crenulatum* (Lamarck) Kunze; 1960, p. 105, pl. 4, Fig. 5; pl. 6, Fig. 12.

Acetabularia farlowii Solms-Laubach

Mexico: Laguna Madre five miles south of eighth pass (Boca Jesus Maria) on the mainland side (west) of the barrier island.

Solms-Laubach 1895, p. 27, pl. III, Fig. 1; Collins 1909, p. 379; Howe 1905, p. 576 (as *Acetabulum farlowii* (Solms) Howe) ; 1960, p. 105; Humm and Taylor 1961, Fig. 9 A-B.

Acetabularia pusilla (Hose) Collins

Mexico: On old shells, *Thalassia* flats on the lee side of Los Hornos inner reef, Vera Cruz.

Howe 1909, p. 89, pl. VI, Fig. 13–15, pl. VII, Fig. 1–4; Collins 1909, p. 379; Taylor 1928, p. 67, pl. 5, Fig. 17–21 (as *Acetabulum pusillum* Howe) ; 1960, p. 104, pl. 6, Fig. 13.

Acicularia schenckii (Möbius) Solms-Laubach

Texas: On shells in Little Bay between Rockport and Fulton.

Solms-Laubach 1895, p. 33, pl. III, Fig. 4, 9, 11, 14; Vickers 1908, p. 29, pl. XLIX (as *Acetabularia caraibica* Kützing) ; Collins 1909, p. 380; Taylor 1928, p. 68, pl. 5, Fig. 8, 26–28; 1960, p. 107, pl. 6, Fig. 11; Humm and Taylor 1961, Fig. 8 A-B, E.

Batophora oerstedi J. Agardh

Texas: On shells and sunken wood, *Thalassia* flats, Aransas Bay about one mile east of the town of Aransas Pass.

J. G. Agardh 1854, p. 108; Collins 1909, p. 303; Taylor 1928, p. 68, pl. 5, Fig. 1, 2, 15, 16; 1960, p. 98, pl. 4, Fig. 3–4; pl. 5, Fig. 4; pl. 6, Fig. 3, 9; Humm and Taylor 1961, Fig. 7 E, J.

Cymopolia barbata (Linnaeus) Lamouroux

Mexico: Abundant on reefs along the coast of Vera Cruz (Blanca reef, Anton Lizardo; Los Hornos reef; an old reef along shore about one mile north of Boca del Rio; at the south end of Isla Sacrificios).

Lamouroux 1816, p. 293; J. Agardh 1886, p. 146; p. 147, pl. 4, Fig. 1–5 (as *C. mex-*

icana) ; Collins 1909, p. 303, Fig. 146; Taylor 1928, p. 69, pl. 5, Fig. 4, 13 and pl. 10, Fig. 11; 1960, p. 102, pl. 4, Fig. 1; pl. 6, Fig. 1.

Family Valoniaceae

Valonia ventricosa J. Agardh

Mexico: Blanquilla reef, Cabo Rojo, Vera Cruz.

J. G. Agardh 1886, p. 96; Vickers 1908, p. 21, pl. XXIII; Collins 1909, p. 293; Taylor 1928, p. 75, pl. 13, Fig. 18; 1960, p. 110, pl. 9, Fig. 4–5.

Chrysophyta

Order Heterosiphonales

Vaucheria sp.

Texas: In shallow water between causeway bridge and ship channel between Port Isabel and Padre Island; on mud-coated rocks, Boca Chica jetty, Brazos Santiago, Cameron County. Sterile. Mexico: Channel side of Punta Hornos, Vera Cruz. Sterile.

Phaeophyta

The classification of Kylin (1933), as modified by Papenfuss (1951), is used in this division.

Order Ectocarpales

Family Ectocarpaceae

Pylaiella antillarum (Grunow) De Toni

Texas: At Cline Point near Port Aransas on shells and woodwork.

Grunow 1867, p. 46, pl. 4, Fig. 2 (as *Ectocarpus antillarum*) ; Bornet 1889, p. 5, pl. 1; De Toni 1895, p. 535 (both as *P. fulvescens* Bornet) ; Vickers 1908, part 2, p. 44, pl. XXXIV (as *P. hooperi* Bornet) ; Blomquist and Humm 1946, p. 5, Fig. 11 (as *P. fulvescens*) ; Blomquist 1958a, Fig. 1–17; Taylor 1960, p. 197.

Ectocarpus elachistaeformis Heydrich

Mexico: On *Codium taylori,* reef at the south edge of Villa del Mar Balneario, Vera Cruz.

Heydrich 1892, p. 470, pl. XXV, Fig. 14; Børgesen 1914, p. 18, Fig. 11; Williams 1948, p. 686, Fig. 7; Taylor 1960, p. 202, pl. 29, Fig. 9.

Ectocarpus siliculosus (Dillwyn) Lyngbye

Texas: On rocks along a sea wall, Laguna Madre near Port Isabel (February). This species is probably present only during the winter months, as is true along the upper Gulf coast of Florida and along the Atlantic coast of the southeastern states to Cape Canaveral, Florida. It is not continuous around the tip of Florida.

Lyngbye 1819, p. 131, pl. 43, Fig. C (excluding variety beta and synonyms) ; Hoyt 1917–18, p. 438, Fig. 8; Hamel 1931–39, p. 21, Fig. 3; Kylin 1947, p. 7, Fig. 2 A, B; Taylor 1960, p. 199.

Ectocarpus variabilis Vickers

Mexico: On *Thalassia* at Punta Hornos, Vera Cruz. Abundant. Although not previously reported from the Gulf of Mexico or from the mainland coasts of North America, it is probably widely distributed in the southern Gulf.

Vickers 1905, p. 59; 1908, part 2, p. 43, pl. XXXI; Børgesen 1920, p. 434, Fig. 410; Taylor 1960, p. 202.

Giffordia mitchellae (Harvey) Hamel

Texas and Mexico: Widely distributed; probably continuous around the Gulf coast. Specimens from *Thalassia* leaves in shallow water between the reef and the beach near Villa del Mar Balneario, Vera Cruz, bore both sporangia and gametangia in January.

Harvey 1852, p. 142, pl. 12, Fig. G; Hoyt 1917–18, p. 439, Fig. 10; Børgesen 1914, p. 6, Fig. 3–4 (all as *Ectocarpus mitchellae*) ; Hamel 1931–39, p. X; Newton 1931, p. 119 (as *E. mitchellae*) ; Taylor 1957, p. 111; 1960, p. 206, pl. 29. Fig. 1–2.

Giffordia duchassaigniana (Grunow) Taylor

Texas: Port Aransas jetty on an old stem of *Leptogorgia;* Rockport, on *Gracilaria foliifera* growing along a seawall; Padre Island jetty and Boca Chica jetty, Brazos Santiago, Cameron County, epiphytic on several larger algae. Undoubtedly along the coast of Mexico and probably continuous around the Gulf.

Grunow 1867, p. 45, pl. 4, Fig. 1; Vickers 1908, part 2, p. 42, pl. XXVII, Fig. 1–8; Børgesen 1914, p. 3, Fig. 1–2; Collins and Hervey 1917, p. 70; Hoyt 1917–18, p. 437, Fig. 7; Taylor 1928, p. 107, pl. 14, Fig. 11; 1942, p. 48 (all as *Ectocarpus duchassaignianus* Grunow) ; 1960, p. 207, pl. 29, Fig. 10.

Giffordia rallsiae (Vickers) Taylor

Texas: On an old stem of *Leptogorgia,* Aransas Pass jetty, and on *Padina vickersiae* at Cline Point, Port Aransas. Mexico: Punta Hornos, Los Hornos reef and jetty, Vera Cruz, epiphytic on larger algae.

Vickers 1905, p. 59; 1908, part 2, p. 44, pl. XXXII; Børgesen 1914, p. 13, Fig. 7; 1926, p. 23, Fig. 11; Collins and Hervey 1917, p. 71 (all as *Ectocarpus rallsiae*) ; Taylor 1960, p. 208.

Order Sphacelariales

Family Sphacelariaceae

Sphacelaria furcigera Kützing

Texas: Shallow water between causeway bridge and ship channel, Port Isabel, on old stems of *Penicillus capitatus;* buoy 119, Laguna Madre channel north of Port Isabel.

Kützing 1845–71, Vol. V (1855), p. 27, pl. 90, Fig. 11; Sauvageau 1901, p. 368, Fig. 35; Vickers 1908, part 2, p. 41, pl. XXV; Lund 1950, p. 29, Fig. 5; Humm and Darnell 1959, p. 272; Taylor 1960, p. 210, pl. 29, Fig. 5.

Sphacelaria tribuloides Meneghini

Mexico: At the south end of Isla Sacrificios, Vera Cruz.

Meneghini 1842, p. 2; Sauvageau 1901, p. 233, Fig. 28; Vickers 1908, part 2, p. 42, pl. XXVI; Blomquist and Humm 1946, p. 5, pl. II, Fig. 15; Lund 1950, p. 42, Fig. 8; Humm and Caylor 1957, p. 246, pl. IV, Fig. 2–4; Taylor 1960, p. 211, pl. 29, Fig. 6.

Family Acinetosporaceae

Acinetospora pusilla (Griffiths) Bornet

Mexico: On *Thalassia* between the reef and the beach near Villa del Mar Balneario, Vera Cruz. Mixed with *Ectocarpus mitchellae.*

Bornet 1891, p. 18; Hamel 1931–39, p. 75, Fig. 22; Børgesen 1926, p. 31, Fig. 15–17 (as *Ectocarpus pusillus* Griffiths) ; Blomquist 1955; Taylor 1960, p. 214.

Order Dictyotales
Family Dictyotaceae

Dictyopteris delicatula Lamouroux

Texas: Boca Chica jetty, Brazos Santiago, Cameron County. One of the most abundant algae on the jetty during the summer months and common during winter also. Mexico: In 3–5 feet of water near Rancho Boca Andrea, Vera Cruz.

Lamouroux 1809a, No. 20, pl. 6, Fig. 8; Vickers 1908, part 2, p. 35, pl. III; Taylor 1928, p. 121, pl. 17, Fig. 7; pl. 19, Fig. 6 (as *Neurocarpus delicatulus* [Lamouroux] Kuntze) ; 1960, p. 227, pl. 33, Fig. 3.

Dictyota bartayresii Lamouroux

Mexico: Common on and near the reefs along the coast of Vera Cruz, including Los Hornos, Giote, Blanca, and others.

This species commonly forms entangled, dense plants in the form of cushions or mats. The dichotomies are wide-angled.

Lamouroux 1809b, p. 43; Vickers 1908, part 2, pl. 35, pls. XII and XIII; Taylor 1928, p. 117, pl. 16, Fig. 16; pl. 19, Fig. 10; 1960, p. 219, pl. 30, Fig. 2.

Dictyota cervicornis Kützing

Mexico: Blanca reef, Anton Lizardo, and off the southwest side of Isla Sacrificios, Vera Cruz.

Kützing 1845–71, 9:11, pl. 24, Fig. II; Taylor 1928, p. 118, pl. 16, Fig. 10, 13, 15, 17; 1960, p. 222, pl. 31, Fig. 2.

Dictyota ciliolata Kützing

Mexico: Giote reef, Anton Lizardo, and Los Hornos reef, Vera Cruz.

One form of this species produces small, erect plants usually 3–4 inches tall with the dichotomies narrow-angled, the branches 2–3 mm wide.

Kützing 1845–71, 9:11, pl. 27; Vickers 1908, part 2, p. 39, pl. XVII (as *D. ciliata* J. Agardh) ; Taylor 1960, p. 223, pl. 32, Fig. 3; pl. 59, Fig. 1.

Dictyota dichotoma (Hudson) Lamouroux

Texas: Aransas Pass jetties and near Cline Point, Port Aransas; in 3–5 feet of water, flats between causeway bridge and ship channel, Port Isabel, and on buoy 119 in the Laguna Madre channel north of Port Isabel. Mexico: Abundant along the coast of Vera Cruz at all stations from which collections were made.

Lamouroux 1809b, p. 42; Hoyt 1917–18, p. 461, pl. XCIV, Fig. 1–3; Humm and Caylor 1957, p. 248, pl. VIII, Fig. 1; Taylor 1960, p. 218, pl. 31, Fig. 5.

Dictyota divaricata Lamouroux

Mexico: Giote reef, Anton Lizardo and Isla Sacrificios, Vera Cruz.

Lamouroux 1809b, p. 43; J. Agardh 1894, p. 101; Collins and Hervey 1917, p. 91; Taylor 1928, p. 120, pl. 16, Fig. 6–9; 1960, p. 221, pl. 31, Fig. 3–4.

Dictyota indica Sonder

Texas: In large masses in 3–5 feet of water between the causeway bridge and ship channel, Port Isabel.

Dictyota dichotoma in typical form occurred in the same habitat and seemed to be readily distinguishable with the exception of occasional plants that were intermediate. Hybridization of two species as similar as these is to be expected, unless their similarity is only superficial. Some experimental field work with plants representing

different species of *Dictyota* is much-needed in order to learn the degree of variation and environmental factors responsible.

Sonder in Kützing, 1845–71, 9:8, pl. XVII; Vickers 1908, part 2, p. 39, pl. XVIII; Taylor 1928, p. 120, pl. 16, Fig. 1; 1960, p. 221, pl. 31, Fig. 1.

Padina gymnospora (Kützing) Vickers

Mexico: On the lee side of Los Hornos reef and at the south end of Isla Sacrificios, Vera Cruz.

Vickers 1905, p. 58; 1908, part 2, p. 37, pl. VII; Børgesen 1914, p. 46, Fig. 29–30; Taylor 1960, p. 237.

Padina sanctae-crucis Børgesen

Mexico: Blanca and Giote reefs, Anton Lizardo, near Rancho Boca Andrea, and at the southwest corner of Isla Sacrificios, Vera Cruz.

Børgensen 1914, p. 45, Fig. 27–28; Taylor 1928, p. 123, pl. 17, Fig. 6; 1960, p. 237, pl. 34, Fig. 2.

Padina vickersiae Hoyt

Texas: On the Aransas Pass jetties, Port Aransas, and on Padre Island and Boca Chica jetties, Brazos Santiago, Cameron County. Mexico: At Punta Hornos and on the lee side and landward end of Los Hornos reef, Vera Cruz.

Hoyt 1917–18, p. 456, Fig. 22, pl. XCII, Fig. 1–2, pl. CXIV, Fig. 1–3; Howe 1920, p. 595 (the original description by Hoyt); Børgesen 1914, p. 49, Fig. 31–33 (as *P. variegata* [Lamouroux] Hauck); Taylor 1960, p. 236, pl. 34, Fig. 1.

Spatoglossum schroederi (Mertens) J. Agardh

Mexico: On the lee side of Los Hornos reef; Giote reef, Anton Lizardo, Vera Cruz. Abundant.

J. Agardh 1880, p. 113, in part; 1894, p. 38; Collins and Hervey 1917, p. 84; Hoyt 1917–18, p. 459 (in part), pl. XCIII, Fig. 1; XCIV, Fig. 2a and b; Taylor 1928, p. 124, pl. 17, Fig. 2; Taylor 1960, p. 225, pl. 33, Fig. 5.

Hoyt's specimens dredged from offshore at Beaufort, N. C., are *S. schroederi*, but his material collected in the harbor is a dentate form of *Dictyota dichotoma* (*fide* Blomquist).

Order Chordariales
Family Chordariaceae

Eudesme zosterae (J. Agardh) Kylin

Mexico: On *Thalassia*, lee side of Los Hornos reef; Blanca reef, Anton Libardo; between the reef and the beach at Villa del Mar Balneario, Vera Cruz. Winter and spring.

Kylin 1940, p. 28 (as *Cladosiphon zosterae* [J. Agardh] Kylin); Hoyt 1917–18, p. 446, pl. LXXXVII, Fig. 1 (as *Castagnea zosterae* [Mohr] Thuret); Taylor 1928, p. 112, pl. 14, Fig. 20–22; pl. 15, Fig. 9 (as *Castagnea*); 1942, p. 49 (as *Aegira zosterae* [Morh] Fries); 1957, p. 146; 1960, p. 247.

Other synonyms include *Mesogloia zosterae* Areschoug and *Myriocladia zosterae* J. Agardh.

Order Dictyosiphonales
Family Myriotrichaceae

Myriotrichia subcorymbosa (Farlow) Blomquist

Texas. On *Diplanthera*, Aransas Bay about one mile east of the town of Aransas Pass;

on *Diplanthera*, Harbor Island, bay side, Nueces County; on a barnacle, nun buoy at the mouth of Arroyo Colorado cutoff, Laguna Madre; buoy 138, Port Isabel harbor. Mexico: On *Thalassia*, Punta Hornos, Vera Cruz; on *Diplanthera* near a creek mouth, Boca Jesus Maria, Tamaulipas.

Collins 1905, p. 227 (as *Ectocarpus subcorymbosus* Farlow); Blomquist 1954, p. 37, pl. 6 (as *Myriotrichia scutata*); 1958a; Taylor 1957, p. 109; 1960, p. 201 (both as *E. subcorymbosus*).

Family Punctariaceae

Colpomenia sinuosa (Roth) Derbes and Solier

Mexico: Widely distributed along the coast of Vera Cruz, especially on the reefs (Blanquilla at Cabo Rojo, Los Hornos, Blanca at Anton Lizardo, an old reef near Boca del Rio).

Derbes and Solier 1856, p. 11, pl. XXII, Fig. 18–20; Collins and Hervey 1917, p. 73; Taylor 1928, pl. 7, p. 110, Fig. 1 and p. 19, Fig. 3–4; Blomquist and Humm, 1946, p. 6, pl. II, Fig. 16–17; Taylor 1960, p. 206, pl. 36, Fig. 1.

Hydroclathrus clathratus (Bory) Howe

Mexico: Blanquilla reef at Cabo Rojo; reef at the south edge of Villa del Mar Balneario; at the southwest corner of Isla Sacrificios, Vera Cruz.

Howe 1920, p. 590; Vickers 1908, part 2, p. 41, pl. XXIII (as *H. cancellatus* Bory); Taylor 1928, p. 110, pl. 15, Fig. 19; pl. 19, Fig. 1; 1960, p. 261, pl. 36, Fig. 5.

Petalonia fascia (Muller) Kuntze

Texas: Jetties of Aransas Pass near Port Aransas, winter and spring only. Possibly the southern limit of the species along the Texas coast, as it was not collected from the Brazos Santiago jetties.

Kuntze 1898, p. 419; Kylin 1933, p. 44, Fig. 17; 1947, p. 77, Fig. 61 (as *Ilea fascia* [Muller] Fries); Taylor 1957, p. 167, pl. 14, Fig. 5; pl. 15, Fig. 3. Silva 1952, discusses the desirability of conserving *Petalonia* rather than *Ilea*, p. 278.

Rosenvingia intricata (J. Agardh) Børgesen

Mexico: On the surf side of Los Hornos reef, Vera Cruz.

J. G. Agardh 1847, p. 7 (as *Asperococcus intricatus*); Børgesen 1914, p. 26; Vickers 1908, part 2, p. 41, pl. XXIV (as *Striaria intricata* [J. Agardh] Vickers); Taylor 1928, p. 111, pl. 15, Fig. 15–17. Vera Cruz is the type locality.

Order Fucales
Family Sargassaceae

Sargassum fluitans Børgesen

Texas and Mexico: This is a strictly pelagic species that drifts ashore, often in abundance, along the entire coastline of the Gulf of Mexico.

Børgesen 1914, p. 66; Taylor 1928, p. 127, pl. 18, Fig. 9 and pl. 19, Fig. 5; Humm and Caylor 1957, p. 249, pl. IX, Fig. 1.

Sargassum hystrix J. Agardh

Var. buxifolium (Chauvin) J. Agardh

Mexico: Common along the shore side of Los Hornos reef.

J. Agardh 1847, p. 7; Howe 1920, p. 594; Taylor 1928, p. 128, pl. 18, Fig. 1 and pl. 19, Fig. 9. The type locality is Campeche Banks.

Sargassum natans (Linnaeus) Meyen

Texas and Mexico: This is a strictly pelagic species that drifts ashore, often in abundance and mixed with *S. fluitans*, along the entire coastline of the Gulf of Mexico. Because of prevailing winds, the pelagic species of *Sargassum* drift ashore in least abundance in the northeastern sector of the Gulf.

Meyen 1838, p. 185; Howe 1920, p. 592; Taylor 1928, p. 128, pl. 18, Fig. 2–4 and pl. 19, Fig. 13; Humm and Caylor 1957, p. 249, pl. IX, Fig. 2.

Sargassum polyceratium Montagne

Mexico: Common on the reefs along the coast of Vera Cruz (Los Hornos, Giote reef at Anton Lizardo, a reef near Rancho Boca Andrea).

Montagne 1837, p. 356; Howe 1920, p. 593; Taylor 1928, p. 129, pl. 18, Fig. 12 and pl. 19, Fig. 14; 1960, p. 276, pl. 40, Fig. 1.

Rhodophyta

The classification and genera of the Rhodoyhyta that follows is from Kylin 1956, with one exception.

Bangioideae

Order Goniotrichales

Family Goniotrichaceae

Asterocystis ornata (C. Agardh) Hamel

Texas: In 3–5 feet of water between the causeway bridge and ship channel, Port Isabel; buoy 49 Laguna Madre channel between Port Isabel and Port Mansfield; jetties at Brazos Santiago, Cameron County. Mexico: Los Hornos reef; an intertidal oyster bar near a creek mouth, Laguna Madre.

Hamel 1924a, p. 451, Fig. VIIB-E; Børgesen 1927, p. 11; Taylor 1928, p. 132, pl. 20, Fig. 1–2 (as *A. ramosa* (Thwaites) Gobi).

Goniotrichum alsidii (Zanardini) Howe

Texas: On *Hypnea* and *Gelidium* from the pilings of the causeway bridge between Port Isabel and Padre Island. Mexico: On *Halimeda tuna* from the southwest corner of Isla Sacrificios, Vera Cruz.

Howe 1914, p. 75; Børgesen 1916, p. 4, Fig. 2 (as *G. elegans* (Chauvin) LeJolis) Hoyt 1917–18, p. 465, Fig. 23; Humm and Caylor 1957, p. 250, pl. VII, Fig. 4; Taylor 1960, p. 288.

Order Bangiales

Family Erythropeltidaceae

Erythrocladia subintegra Rosenvinge

Texas: On *Dictyota* and *Padina*, Aransas Pass jetties at Port Aransas. Mexico: On *Cladophora fascicularis* between the reef and the beach and on *Chaetomorpha media* from the south edge of the reef, Villa del Mar Balneario, Vera Cruz.

Rosenvinge 1909, p. 73, Fig. 13–14; Børgesen 1916, p. 7; Fig. 3–4; Taylor 1928, p. 132, pl. 20, Fig. 3; 1960, p. 290, pl. 41, Fig. 1.

Family Bangiaceae

Bangia fuscopurpurea (Dillwyn) Lyngbye

Texas: Abundant high in the intertidal zone, north jetty at Brozos Santiago, Cameron County, February.

Lyngbye 1819, p. 83; Hoyt 1917–18, p. 464; Collins and Hervey 1917, p. 94; Taylor 1957, p. 204, pl. 28, Fig. 10–12; 1960, p. 293.

Florideae

Order Nemalionales

Family Chantransiaceae

Kylinia crassipes (Børgesen) Kylin

Mexico: On *Hypnea musciformis* from the lee side of Los Hornos reef, Vera Cruz.

Børgesen 1910a, p. 1, Fig. 1; 1916, p. 20, Fig. 11–13; Humm and Caylor 1957, p. 250, pl. VII, Fig. 8, all as *Achrochaetium crassipes* Børgesen; Taylor 1960, p. 300.—

Achrochaetium flexuosum Vickers

Texas. On old stem of *Leptogorgia,* Aransas Pass jetty, Port Aransas.

Vickers 1905, p. 60; Børgesen 1916, p. 34, Fig. 29–30; Taylor 1960, p. 308.

Achrochaetium hoytii Collins

Texas: On *Dictyota dichotoma* from near Cline Point.

Collins 1908, p. 134; Hoyt 1917–18, p. 470, Fig. 27–28; Taylor 1960, p. 306.

Achrochaetium sagraeanum (Montagne) Bornet

Mexico: On *Thalassia* between the reef and the beach, Villa del Mar Balneario, Vera Cruz.

Bornet 1904, p. XXI; Collins and Hervey 1917; Taylor 1960. p. 309.

Achrochaetium seriatum Børgesen

Texas. On *Diplanthera,* Aransas Bay about one mile east of the town of Aransas Pass; on *Gelidium crinale* and *Gracilaria foliifera* along the seawall at Rockport; buoy 119, Laguna Madre channel just north of Port Isabel.

Børgesen 1916, p. 32, Fig. 25–28; Humm and Caylor 1957, p. 250, pl. VII, Fig. 5; Taylor 1960, p. 310.

Family Helminthocladiaceae

Liagora mucosa Howe

Mexico: On a calcareous sand bottom, Blanca reef, Anton Lizardo, Vera Cruz, April.

Howe 1920, p. 556; Taylor 1928, p. 136; 1960, p. 328.

Trichogloea requienii (Montagne) Kützing

Mexico: On the shoreward side of Los Hornos reef, Vera Cruz. This seems to be the first report from the Gulf of Mexico.

Kützing 1847, p. 53; Taylor 1960, p. 323.

Family Chaetangiaceae

Galaxaura lapidescens (Ellis and Solander) Lamouroux

Mexico: Blanquilla reef, Cabo Rojo, Vera Cruz.

Lamouroux 1816, p. 264; Børgesen 1916, p. 95, Fig. 102–104; Taylor 1928, p. 138, pl. 21, Fig. 13 and pl. 30, Fig. 8; 1960, p. 337.

Galaxaura rugosa (Ellis and Solander) Lamouroux

Mexico: At the south end of Isla Sacrificios and on the surf side of Los Hornos reef, Vera Cruz, April.

Lamouroux 1816, p. 263; Børgesen 1916, p. 100, Fig. 105–107; Taylor 1928, p. 140, pl. 21, Fig. 16 and pl. 30, Fig. 2, 10; 1960, p. 340.

Galaxaura squalida Kjellman

Mexico: At the southwest corner of Isla Sacrificios and and Blanquilla reef, Cabo Rojo, Vera Cruz, April and May.

Kjellman 1900, p. 55, pl. 6, Fig. 1–12, pl. 20, Fig. 9; Børgesen 1916, p. 102, Fig. 110–111; Taylor 1928, p. 140, pl. 21, Fig. 18 and pl. 31, Fig. 4; 1960, p. 339, pl. 44, Fig. 3; pl. 45, Fig. 6.

Galaxaura stellifera J. Agardh

Mexico: On the shoreward side of Los Hornos reef, Vera Cruz, April. Taylor (1960) suggests that this may be a form of *G. cylindrica* (Ellis and Solander) Lamouroux.

J. G. Agardh 1884, p. 73; Kjellman 1900, p. 73; Taylor 1928, p. 141; 1960, p. 346.

Order Gelidiales

Family Gelidiaceae

Gelidium corneum (Hudson) Lamouroux

Texas: In almost pure stands on upper rocks along the seawall at Rockport; on the Aransas Pass jetties, Port Aransas; on the bridge supports, causeway between Port Isabel and Padre Island; on rocks at the base of a retaining wall, Laguna Madre channel at Port Isabel; on the jetties at Brazos Santiago, Cameron County. Mexico: Blanca reef and Giote reef, Anton Lizardo; on an old reef along shore one mile north of Boca del Rio; and at Rancho Boca Andrea, Vera Cruz.

Lamouroux 1813, p. 129; Børgesen 1916, p. 114, Fig. 124; Taylor 1928, p. 142, pl. 28, Fig. 2; Hoyt 1917–18, p. 475, pl. XCV, Fig. 1 (as *G. coerulescens* Kützing); Humm and Caylor 1957, p. 252, pl. VII, Fig. 7.

Gelidium crinale (Turner) J. Agardh

Texas: Boca Chica and Padre Island jetties, Brazos Santiago, Cameron County. Abundant on the channel side.

J. G. Agardh 1876, p. 546; Hoyt 1917–18, p. 475, pl. XCV, Fig. 2; Feldmann and Hamel 1936, p. 116, Fig. 22(p. 241), pl. I, Fig. 1.

Gelidium pusillum (Stackhouse) LeJolis

Mexico: Los Hornos reef jetty (mixed with *Amphiroa rigida*) and on top of the reef south of the jetty, Vera Cruz.

Le Jolis 1863, p. 139; Taylor 1928, p. 142, pl. 20, Fig. 8, pl. 22, Fig. 7 and pl. 23, Fig. 3; Feldmann and Hamel 1936, p. 112, Fig. 19, 20; Joly 1957, p. 99, pl. IX, Fig. 4 and pl. X, Fig. 5.

Order Cryptonemiales

Family Hildenbrandtiaceae

Hildenbrandtia prototypus Nardo

Mexico: Blanca reef and Giote reef, Anton Lizardo. On shells.

Nardo 1834, p. 675; Børgesen 1916–20, p. 146; Kylin 1944, p. 36, Fig. 30; Dawson

1953, p. 95, pl. 7, Fig. 4; Taylor 1957, p. 241, pl. 36, Fig. 9–10; Joly 1957, p. 105, pl. XIX, Fig. 2, 2a.

Family Corallinaceae

Porolithon børgesenii (Foslie) Lemoine

Mexico: On limestone rocks in an exposed locality, Los Hornos reef, Vera Cruz.

Foslie 1900, p. 19 (as *Goniolithon borgesenii*); Lemoine in Børgesen 1916–20, p. 178, Fig. 168–169; Taylor 1960, p. 397, pl. 76, Fig. 2 (as *G. borgesenii*).

Lithophyllum pustulatum (Lamouroux) Foslie

Texas: On the older parts of *Gelidium corneum*, Aransas Pass jetty. Mexico: On *Thalassia*, Blanca reef, Anton Lizardo, Vera Cruz.

Foslie 1904, p. 3; Suneson 1943, p. 39, textfigs. 22–23, pl. VI, Fig. 26–27; pl. VIII, Fig. 37; Kylin 1944, p. 42, pl. 7. Fig. 23; Taylor 1960, p. 392.

Fosliella farinosa (Lamouroux) Howe

Texas: On Thalassia, Aransas Bay; on *Padina*, *Rhodymenia*, and other algae, Boca Chica and Padre Island jetties, Brazos Santiago, Cameron County.

Lamouroux 1816, p. 315; Rosanoff 1866, p. 69, pl. II, 3–5, 10–12; pl. III, Fig. 2–3; pl. IV, Fig. 10; pl. VII, Fig. 12; Lemoine in Børgesen 1916–20, p. 170, Fig. 165; Hoyt 1917–18, p. 573 (all as *Melobesia farinosa*); Howe 1920, p. 587; Taylor 1960, p. 388.

Heteroderma lejolisii (Rosanoff) Foslie

Texas and Mexico: Probably at all stations from which collections reported here were made, as an epiphyte on *Thalassia* and algae.

Rosanoff 1866, p. 62 (as *Melobesia lejolisii*); Howe 1920, p. 588; Taylor 1960, p. 387 (as *Fosliella lejolisii* (Rosanoff) Howe); Suneson 1943, p. 23, tevt fig. 13A; pl. 4, Fig. 18, pl. 5, Fig. 21 (as *Melobesia*); Joly 1957, p. 108, pl. X, Fig. 11; pl. XII, Fig. 2 (as *Fosliella*); Dawson 1960, p. 55, pl. 50, Fig. 4–6.

Amphiroa fragilissimi (Linnaeus) Lamouroux

Texas: In large masses in 3–5 feet of water between the causeway bridge and ship channel, Port Isabel. Abundant. Mexico: Los Hornos reef and breakwater, Isla Sacrificios, Vera Cruz.

Lamouroux 1816, p. 298; Børgesen 1916–20, p. 185; Taylor 1960, p. 403, pl. 47, Fig. 1–2.

Amphiroa rigida Lamouroux

variety *antillana* Børgesen

Mexico: At the south end of Los Hornos reef jetty and on the reef itself, Vera Cruz.

Lamouroux 1816, p. 297, pl. XI, Fig. 1; Børgesen 1916–20, p. 182, Fig. 171–173; Taylor 1960, p. 404, pl. 47, Fig. 3; pl. 48, Fig. 1.

Jania capillacea Harvey

Mexico: Los Hornos reef and breakwater, and at the south end of Isla Sacrificios, Vera Cruz.

Harvey 1853, p. 84; Børgesen 1916–20, p. 198, Fig. 188; Taylor 1960, p. 412, pl. 49, Fig. 4.

Jania decussato-dichotoma (Yendo) Yendo

Texas: Washed ashore, bay side of Padre Island near Brazos Santiago, Cameron County.

Dawson (1953) points out that *Jania adhaerens* Lamouroux, with which this material might otherwise have been associated, should be rejected from current and future literature because of the lack of an adequate description, a type specimen, an authentic illustration, and the unknown source of the original collection. In order to determine if the material previously referred to *J. adhaerens* by several algologists who collected in the western North Atlantic should be referred to *J. decussato-dichotoma*, restudy of specimens is necessary and comparison with Pacific material. Consequently, this determination is tentative.

Lamouroux 1816, p. 270; Yendo 1902, p. 25, pl. 3, Fig. 1–3; pl. 7, Fig. 3–4; Børgesen 1917, p. 195, Fig. 184–187; Howe 1920, p. 589; Taylor 1928, p. 205; 1960, p. 413, pl. 49, Fig. 1–2 (all as *J. adhaerens* except Yendo and Dawson).

Jania rubens (Linnaeus) Lamouroux

Texas: On the Gulf side of Boca Chica jetty, Brazos Santiago, Cameron County. Mexico: Los Hornos reef and breakwater and at the south end of Isla Sacrificios, Vera Cruz.

Lamouroux 1812, p. 186; Kützing 1843, p. 389, pl. 79, Fig. 2; Taylor 1928, p. 206, pl. 29, Fig. 3–6; Kylin 1944, p. 47, pl. IX, Fig. 33; Joly 1957, p. 112, pl. XI, Fig. 4, 4a, 4d; Taylor 1960, p. 413, pl. 49, Fig. 3.

Corallina subulata Ellis and Solander

Texas: Jetties at Aransas Pass and at Brazos Santiago. Mexico: On an old reef along shore about one mile north of Boca del Rio, Vera Cruz. Not previously reported for Texas.

Ellis and Solander 1786, p. 119, pl. 21, Fig. B, b; Howe 1920, p. 589; Taylor 1960, p. 410, pl. 50, Fig. 1–2.

Family Grateloupiaceae

Halymenia floridana J. Agardh

Texas: At the seaward end of the west jetty of Aransas Pass, Port Aransas.

J. Agardh 1894, p. 59; Hoyt 1917–18, p. 519, Fig. 45, 46 (p. 519) and pl. CXII, Fig. 4b; Taylor 1960, p. 420, pl. 52, Fig. 2.

Grateloupia filicina (Wulfen) C. Agardh

Texas: Jetties at Brazos Santiago, Cameron County, where abundant; bouy 129 in the harbor at Port Isabel. Mexico: Reef at the south edge of Villa del Mar Balneario.

C. Agardh 1822, p. 223; Hoyt 1917–18, p. 521, pl. CXIII, Fig. 1; Børgesen 1916–20, p. 123; Joly 1957, p. 120, pl. VIII, Fig. 5; Humm and Caylor 1957, p. 252; Taylor 1960, p. 424, pl. 54, Fig. 2–3.

Order Gigartinales

Family Gracilariaceae

Gracilaria armata (C. Agardh) J. Agardh

Texas: On *Diplanthera* flats in shallow water at the western edge of Port Isabel. Mexico: In the Laguna Madre about three miles south of Point of Rocks on the eastern shore of the peninsula.

J. G. Agardh 1847, p. 15; Harvey 1853, p. 109; Børgesen 1929, p. 82; Funk 1955, p. 79; Taylor 1960, p. 441.

Gracilaria blodgettii Harvey

Texas: In shallow water between the causeway bridge and ship channel, Port Isabel. Occasional and loose, prevented from drifting by *Thalassia.* Mexico: Lee side of Los Hornos reef, Vera Cruz.

Harvey 1853, p. 111; Taylor 1928, p. 151, pl. 23, Fig. 9; pl. 33, Fig. 6; 1960, p. 449, pl. 56, Fig. 1.

Gracilaria caudata J. Agardh

Texas: On *Diplanthera* flats in shallow water at the western edge of Port Isabel. Mexico: In the Laguna Madre about three miles south of Point of Rocks, eastern shore of the peninsula; on an old reef parallel to the shore about one mile north of Boca del Rio, Vera Cruz.

J. Agardh 1852, p. 598; Harvey 1853, p. 111; Børgesen 1916–20, p. 375, Fig. 363.

Gracilaria debilis (Forsskal) Børgesen

Mexico: At the south end of Los Hornos reef jetty; at Punta Hornos, reef at the south edge of Villa del Mar Balneario, Vera Cruz.

Børgesen 1932, p. 9; and the following as *G. cornea* J. Agardh: Howe 1920, p. 563; Taylor 1928, p. 152, pl. 23, Fig. 6; pl. 36, Fig. 4.

Gracilaria domingensis Sonder

Mexico: Shoreward side of Los Hornos reef, Vera Cruz.

Sonder in Kützing 1845–71, 19:8, pl. 22, Fig. a and b; Collins 1901, p. 254; Mazza 1905–11, p. 183 (Sp. No. 171); Taylor 1960, p. 446, pl. 57, Fig. 1–2.

Gracilaria ferox J. Agardh

Texas: Buoy 138, Port Isabel harbor.

J. G. Agardh 1852, p. 592; Børgesen 1916–20, p. 374; Taylor 1928, p. 154, pl. 33, Fig. 2; 1960, p. 444, pl. 56, Fig. 4.

Gracilaria foliifera (Forsskal) Børgesen

Texas: Widely distributed. Rockport, jetties at Port Aransas and Brazos Santiago, Laguna Madre and Port Isabel harbor. Mexico: Los Hornos reef and jetty, Punta Hornos, Laguna Madre and other reef stations.

Harvey 1853, p. 107; Hoyt 1917–18, p. 484, pl. XCIV, Fig. 2 (both as *G. multipartita* (Clemente) J. Agardh); Børgesen 1932, p. 7, Fig. 1; Taylor 1960, p. 446, pl. 55, Fig. 1. (Not *G. lacinulata* (Vahl) Howe.)

Gracilariopsis sjoestedtii (Kylin) Dawson

Mexico: Attached to annelid tubes (*Diopatra*) in shallow water near Villa del Mar Balneario, and in Estero de Mandingo about 250 meters above the bridge, Vera Cruz.

Kylin 1930, p. 55, Fig. 40E, F, 41, 43; Dawson 1949, p. 40, pl. 15, Fig. 10; pl. 16, Fig 5–8; pl. 17; pl. 18, Fig. 4.

Family Solieriaceae

Agardhiella tenera (J. Agardh) Schmitz

Texas: On the jetties of Aransas Pass at Port Aransas and the jetties at Brazos Santiago, Cameron County. Mexico: Common on the reefs along the coast of Vera Cruz.

Harvey 1853, p. 121, pl. XXIIIA (as *Solieria chordalis*); Schmitz 1889, p. 441; Børgesen 1916–20, p. 361, Fig. 355–357; Taylor 1957, p. 267, pl. 38, Fig. 4; pl. 40, Fig. 7; pl. 41, Fig. 2; pl. 59, Fig. 9.

Family Hypneaceae

Hypnea cervicornis J. Agardh

Mexico: In the Laguna Madre about three miles south of Point of Rocks on the east shore of the peninsula, and on Los Hornos reef, Vera Cruz.

J. G. Agardh 1852, p. 451; Collins and Hervey 1917, p. 112; Børgesen 1916–20, p. 383; Taylor 1928, p. 156, pl. 22, Fig. 11.

Hypnea cornuta (Lamouroux) J. Agardh

Mexico: On *Thalassia*, Punta Hornos, and on Los Hornos reef, Vera Cruz.

J. G. Agardh 1852, p. 449; Harvey 1853, p. 125; Taylor 1928, p. 156, pl. 22, Fig. 12.

Hypnea musciformis (Wulfen) Lamouroux

Texas and Mexico: At virtually all stations from which these collections were made.

Lumouroux 1813, p. 131; Hoyt 1917–18, p. 485, pl. C. and pl. CI, Fig. 1, 2; Taylor 1928, p. 156, pl. 22, Fig. 10 and pl. 23, Fig. 12.

Hypnea alopecuroides Kützing, the type area of which is Vera Cruz, is regarded by Taylor (1960) as a synonym of *H. musciformis*. A study of the genus is needed to determine the extent of variation with habitat of the species ordinarily recognized.

Order Rhodymeniales

Family Rhodomeniaceae

Rhodymenia pseudopalmata (Lamouroux) Silva

Texas: On the jetties at Aransas Pass, Port Aransas, and at Brazos Santiago. Common just below spring low tide or a little higher where shaded by overhanging rocks. While most of the plants were sterile, a few tetrasporic specimens were found. On this basis, the assumption was made that all belong to this species rather than to the macroscopically similar *Leptofauchea rhodymenioides* Taylor.

Silva 1952, p. 265; and the following as *R. palmetta* (Esper) Greville: Greville 1830, p. 88, pl. 12; Hoyt 1917–18, p. 487, pl. CI, Fig. 3 and 4.

Family Lomentariaceae

Lomentaria uncinata Meneghini

Texas: On *Dictyota* in shallow water between the causeway bridge and ship channel, Port Isabel; on the jetties of Aransas Pass at Port Aransas. Mexico: At the top of an annelid tube (*Diopatra*) at Punta Hornos, Vera Cruz.

Though this may not be the proper name, it seems unlikely that this small warm-water form is conspecific with the large, bushy-branched plant of New England and Beaufort, N. C., (winter and spring).

Meneghini in Zanardini 1840, p. 215; Hoyt 1917–18, p. 492, pl. CIV, Fig. 2; Collins and Harvey 1917, p. 115; Taylor 1928, p. 161, pl. 22, Fig. 17; 1960, p. 487 (as *L. baileyana* (Harvey) Farlow).

Champia parvula (C. Agardh) Harvey

Texas: On *Thalassia* in Aransas Bay about one mile east of the town of Aransas Pass. Mexico: On *Thalassia* at Punta Hornos; Giote reef at Anton Lizardo, Vera Cruz. The Mexican plants all variety *prostrata* Williams.

Harvey 1853, p. 76; Hoyt 1917–18, p. 493, pl. CIV, Fig. 4; Taylor 1928, p. 158, pl. 24, Fig. 3; 1960, p. 490, pl. 61, Fig. 4.

Order Ceramiales

Family Ceramiaceae

Ceramium gracillium (Griffiths) Harvey
variety *byssoideum* (Harvey) Mazoyer
Texas and Mexico: At virtually all stations from which these collections were made. Harvey 1853, p. 218 (as *C. byssoideum* Harvey); Collins and Hervey 1917, p. 145, pl. V, Fig. 29–31 (as *C. transversale* Collins and Hervey); Taylor 1928, p. 190, pl. 27, Fig. 20, 21 (as *C. byssoideum*); Mazoyer 1938, p. 323; Feldmann-Mazoyer 1940, p. 293, Fig. 109.

Ceramium corniculatum Montagne
Mexico: Los Hornos reef, lee side, and breakwater at the north end of the reef.
Montagne 1860, p. 172 pl. 11B, Fig. 1–3; Howe 1920, p. 583; Taylor 1928, p. 191; 1960, p. 530.

Ceramium fastigiatum (Roth) Harvey
Forma flaccida Petersen
Texas: On bridge supports of the causeway from Port Isabel to Padre Island; on oyster shells and on buoy 119, Laguna Madre channel just north of Port Isabel. Mexico: Breakwater at the north end of Los Hornos reef and in the Laguna Madre of Mexico just south of Point of Rocks.
Harvey 1834, p. 303; J. Agardh 1851, p. 119; Børgesen 1916–20, p. 241, Fig. 231 (forma flaccida Petersen); Taylor 1928, p. 191, pl. 27, Fig. 12–16; Taylor 1957, p. 309, pl. 47, Fig. 3–5, 7; pl. 48, Fig. 2–4; pl. 49, Fig. 3–4; pl. 50, Fig. 4; pl. 51, Fig. 6–7; 1960, p. 526, pl. 67, Fig. 4–6.

Ceramium subtile J. Agardh
Mexico: On *Thalassia*, lee side of Los Hornos reef, Vera Cruz.
J. Agardh 1851, p. 120; Howe 1920, p. 582; Taylor 1928, p. 192, pl. 27, Fig. 17–19; 1960, p. 527, pl. 65, Fig. 5–6.

Centroceras clavulatum (C. Agardh) Montagne
Texas and Mexico: At virtually all stations from which collections were made except for parts of the Laguna Madre. On the jetties of Aransas Pass this species shares dominance at the upper level with *Ulva fasciata*.
Montagne 1846, p. 149; Børgesen 1918, p. 241; Taylor 1928, p. 189, pl. 28, Fig. 6–7; 1960, p. 537.

Spyridia aculeata (Scrimper) Kützing
Texas: On the jetties of Aransas Pass at Port Aransas and at Brazos Santiago; buoy 129 in the harbor at Port Isabel.
Kützing 1843, p. 377; Børgesen 1916–20, p. 237, Fig. 228–230; Blomquist and Humm 1946, p. 7, pl. III, Fig. 26–29; Taylor 1960, p. 541, pl. 66, Fig. 16; pl. 71, Fig. 5.

Spyridia clavata Kützing
Texas: Boca Chica jetty and Padre Island jetty, Brazos Santiago, Cameron County. Mexico: From an old reef along shore about one mile north of Boca del Rio, Vera Cruz.
Kützing 1841, p. 744; 1843, p. 377; 1849–69, 12:14 (No. 2979), pl. 45 c, d; Børgesen 1916–20, p. 235, Fig. 227; Hoyt 1917–18, p. 513; Taylor 1960, p. 541.

Spyridia filamentosa (Wulfen) Harvey

Texas: Rattlesnake Point, Copano Bay; *Halodule* flats in 1–2 feet of water at the western edge of Port Isabel. Mexico: In the Laguna Madre near Point of Rocks and on an oyster bar near a creek mouth.

Harvey 1834, p. 336; Kützing 1843, p. 376, pl. 48, Fig. 1–5; Børgesen 1916–20, p. 233, Fig. 222–226; Hoyt 1917–18, p. 512, pl. CXI, Fig. 1; Taylor 1928, p. 197, pl. 28, Fig. 4, 18; 1960, p. 539, pl. 66, Fig. 15.

Wrangelia argus Montagne

Mexico: On the upper parts of the cushions of *Amphiroa fragilissima,* breakwater at the north end of Los Horons reef; Giote reef, Anton Lizardo; Vera Cruz.

Montagne 1856, p. 444; Børgesen 1916–20, p. 116, Fig. 125–126; Taylor 1928, pl. 20, Fig. 13; pl. 22, Fig. 6; pl. 32, Fig. 4; 1960, p. 502, pl. 66, Fig. 7–8.

Callithamnion byssoides Arnott

Texas: On the jetties at Brazos Santiago, Cameron County; on bridge supports of the causeway between Port Isabel and Padre Island (on *Hypnea* and *Gelidium*).

Arnott in Hooker 1833, Vol. II, part 1, p. 342; Børgesen 1916–20, p. 218, Fig. 205–207; Taylor 1928, p. 189; 1960, p. 506.

Callithamnion corymbosum (Smith) Lyngbye

Texas: On *Padina vickersiae,* Gulf side of Boca Chica jetty, Brazos Santiago, Cameron County.

Lyngbye 1819, p. 125, pl. 38C; Collins and Hervey 1917, p. 136; Kylin 1944, p. 73; Funk 1955, p. 133; Taylor 1960, p. 507.

Callithamion halliae Collins

Mexico: On *Cymopolia barbata,* Blanca reef, Anton Lizardo, Vera Cruz.

Collins 1906, p. 111; Collins and Hervey 1917, p. 136; Taylor 1928, p. 189; 1960, p. 505.

Family Delesseriaceae

Taenioma macrourum Thuret

Mexico: Mixed with *Wrangelia argus* growing on top of dense cushions of *Amphiroa fragilissima* on the breakwater at the north end of Los Hornos reef, Vera Cruz. Not previously known from the Gulf of Mexico.

Thuret in Bornet and Thuret 1876–80, p. 69, pl. 25; Taylor 1960, p. 548.

Family Dasyaceae

Dasya pedicellata (A. Agardh) C. Argardh

Mexico: Giote reef, Anton Lizardo, mixed with *Agardhiella* and *Spatoglossum;* near Rancho Boca Andrea; Vera Cruz.

C. Agardh 1824, p. 211; Kützing 1843, p. 414, pl. 51, Fig. 5–6 (as *D. elegans*); Børgesen 1916–20, p. 316; Taylor 1957, p. 326; 1960, p. 562.

Dasya rigidula (Kützing) Ardissone

Texas: Buoy 129 in the harbor at Port Isabel.

Ardissone 1878, p. 140; Howe 1920, p. 576; Taylor 1928, p. 174, pl. 26, Fig. 2; 1960, p. 558, pl. 72, Fig. 4.

Family Rhodomelaceae

Polysiphonia binneyi Harvey

Mexico: Los Hornos reef, Giote reef at Anton Lizardo, and a reef at the south edge of Villa del Mar Balneario, Vera Cruz.

Harvey 1853, p. 37; Taylor 1928, p. 183; 1960, p. 577.

Polysiphonia denudata (Dillwyn) Kützing

Texas: Buoy 119, Laguna Madre channel just north of Port Isabel. Mixed with *Polysiphonia ferulacea.*

Kützing 1849, p. 824; Hoyt 1917–18, p. 503, Fig. 41B (p. 504); pl. CVIII, Fig. 4a, b; pl. CIX, Fig. 1 and 2; Taylor 1957, p. 339, pl. 56, Fig. 3; pl. 57, Fig. 6–10; pl. 59, Fig. 1; 1960, p. 580.

Polysiphonia ferulacea Suhr

Texas: On the jetties at Brazos Santiago, Cameron County; on buoys 119 and 129 in the harbor at Port Isabel. Mexico: Los Hornos reef, and on an old reef along shore about one mile north of Boca del Rio, Vera Cruz.

J. G. Agardh 1863, p. 980; Collins and Hervey 1917, p. 124; Børgesen 1916–20, p. 277, Fig. 277–280; Taylor 1928, p. 183, pl. 24, Fig. 16–18; pl. 25, Fig. 15; pl. 26, Fig. 11, 15; 1960, p. 578.

This species was collected at Vera Cruz by Liebmann in 1845.

Polysiphonia gorgoniae Harvey

Mexico: On *Thalassia* at Punta Hornos, Vera Cruz.

Harvey 1853, p. 39; Howe 1920, p. 570; Taylor 1928, p. 184; 1960, p. 576.

Polysiphonia hapalacantha Harvey

Texas: On roots of black mangroves at the edge of the ship channel near Port Isabel; Harbor Island near the causeway, Nueces County.

Harvey 1853, p. 39; Howe 1920, p. 570; Taylor 1928, p. 184; 1960, p. 579.

Polysiphonia havanensis Montagne

Texas: On *Diplanthera* in Aransas Bay about one mile east of the town of Aransas Pass; on *Diplanthera* bay side of Harbor Island, Nueces County; on the jetties at Brazos Santiago, Cameron County, in the harbor at Port Isabel. Mexico: Los Hornos reef and the Laguna Madre.

Montagne 1837, p. 352; Børgesen 1916–20, p. 266, Fig. 259–261; Howe 1920, p. 570; Taylor 1928, p. 184; 1960, p. 577.

Polysiphonia howei Hollenberg

Texas: On bridge supports of the causeway between Port Isabel and Padre Island; on buoys in the harbor of Port Isabel and in the Laguna Madre near Port Mansfield.

Børgesen 1916–20, p. 294, Fig. 292–294 (as *Lophosiphonia obscura* (C. Agardh) Falkenberg); Howe 1920, p. 574 (as *L. obscura* Auct.); Hollenberg in Taylor 1945, p. 302, Fig. 3; Joly 1957, p. 164, pl. XIII, Fig. 5, 5a; Taylor 1960, p. 582.

Polysiphonia macrocarpa Harvey

Texas: On *Diplanthera* in Aransas Bay about one mile east of the town of Aransas Pass. Mexico: Los Hornos reef and Blanquilla reef at Cabo Rojo (on *Colpomenia*), Vera Cruz.

Harvey in Mackay 1836, part 2, p. 206; Collins and Hervey 1917, p. 123; Børgesen 1916–20, p. 274, Fig. 272–276; Taylor 1928, p. 184; 1960, p. 578.

Polysiphonia ramentacea Harvey

Texas: Rattlesnake Point, Copano Bay.

Harvey 1853, p. 42, pl. 16A; Howe 1920, p. 570; Taylor 1928, p. 185, pl. 25, Fig. 13 and pl. 26, Fig. 16; 1960, p. 580.

Polysiphonia subtilissima Montagne

Texas: On *Digenea simplex* from *Diplanthera* flats at the west edge of Port Isabel. Mexico: Isla Martinica, Laguna de Tamiahua.

Montagne 1840, p. 199; Howe 1920, p. 570; Taylor 1928, p. 185, pl. 25, Fig. 14 and pl. 26, Fig. 14; Funk 1955, p. 136, pl. XXII, Fig. 3, 5; Taylor 1960, p. 575.

Bryocladia cuspidata (J. Agardh) De Toni

Texas: On the jetties of Aransas Pass, especially among the deeper algae; abundant on the jetties at Brazos Santiago, Cameron County; on buoys in the harbor, Port Isabel. Mexico: Near Rancho Boca Andrea and on an old reef along shore about one mile north of Boca del Rio, Vera Cruz.

J. Agardh 1847, p. 16 (as *Polysiphonia cuspidata* J. Agardh); Taylor 1928, p. 168; 1960, p. 586, pl. 71, Fig. 2.

Bryothamnion triquetrum (Gmelin) Howe

Mexico: On an old reef along shore about one mile north of Boca del Rio, Vera Cruz.

Howe 1915, p. 222; 1920, p. 571; Børgesen 1916–20, p. 282, Fig. 282–283; Taylor 1928, p. 169, pl. 26, Fig. 10; 1960, p. 587, pl. 72, Fig. 6; pl. 73, Fig. 4.

Digenia simplex (Wulfen) C. Agardh

Texas: Near Cline Point; Aransas Bay on sea grass flats; on Diplanthera flats at the western edge of Port Isabel. Mexico: Blanca reef, Anton Lizardo, Vera Cruz.

C. Agardh 1822, p. 388; Collins and Hervey 1917, p. 124; Howe 1920, p. 569; Taylor 1928, p. 175, pl. 24, Fig. 20 and pl. 33, Fig. 7; Funk 1955, p. 138; Humm and Darnell 1960, p. 274.

Herposiphonia pecten-veneris (Harvey) Falkenberg

Mexico: On the surf side of Los Hornos reef, Vera Cruz.

Falkenberg 1901, p. 315; Collins and Hervey 1917, p. 126; Howe 1920, p. 573; Taylor 1928, p. 176; 1960, p. 603.

Herposiphonia secunda (C. Agardh) Ambronn

Texas: On the jetties at Port Aransas, generally below low tide.

Ambronn 1880, 197, pl. 4, Fig. 8, 12; Falkenberg 1901, p. 307, pl. III, Fig. 10–12; Collins and Hervey 1917, p. 126; Børgesen 1916–20, p. 469, Fig. 428–429; Howe 1920, p. 574; Taylor 1928, p. 176, pl. 25, Fig. 8–10; 1960, p. 604, pl. 72, Fig. 10–11.

Herposiphonia tenella (C. Agardh) Ambronn

Texas: On the jetties at Port Aransas; on Digenia at Cline Point; on the jetties at Brazos Santiago, Cameron County.

Nägeli 1846, p. 238, pl. VII, Fig. 2; Ambronn 1880, p. 197, pl. 4, Fig. 9, 11, 13–16; Collins and Hervey 1917, p. 126; Howe 1920, p. 573; Børgesen 1916–20, p. 286; 1920, p. 472, Fig. 430; Taylor 1928, p. 177, pl. 25, Fig. 11; 1960, p. 604, pl. 72, Fig. 12.

Falkenbergia hillebrandii (Bornet) Falkenberg

Mexico: Giote reef, Anton Lizardo, Vera Cruz.

Falkenberg 1901, p. 689; Collins and Hervey 1917, p. 122; Børgesen 1916–20, p. 331, Fig. 332–333; Howe 1920, p. 577; Taylor 1928, p. 175, pl. 25, Fig. 4–5; 1960, p. 571, pl. 72, Fig. 8.

J. and G. Feldman (1942) state that the carpospores of *Asparagopsis armata* Harvey germinate into plants of *Falkenbergia rufolanosa* (Harvey) Schmitz. Tetraspores have been observed in *Falkenbergia* but no gametangia or procarps. *Falkenbergia* seems to occur in some localities where *Asparagopsis* does not (the Florida keys, for example). Further studies on the cytology and life history of these genera are needed.

Chondria curvilineata Collins and Hervey

Texas: On bridge supports, causeway between Port Isabel and Padre Island and on on flats between the causeway and ship channel (on *Thalassia*); on buoy 119 in the Laguna Madre channel north of Port Isabel and on buoys in the harbor.

Collins and Hervey 1917, p. 120, pl. II, Fig. 10–11; Howe 1920, p. 568; Taylor 1960, p. 617.

Chondria leptacremon (Melville) De Toni

Mexico: On *Thalassia* at Punta Hornos, Vera Cruz.

Melvill in Murray 1888, p. 333, pl. 284, Fig. 2a, b; Howe 1920, p. 568; Humm and Caylor 1957, p. 256, pl. VII, Fig. 10; Taylor 1960, p. 615.

Chondria littoralis Harvey

Mexico: On the lee side of Los Hornos reef, Vera Cruz.

Harvey 1853, p. 23; Hoyt 1917–18, p. 499, Fig. 36–37 (p. 504), pl. CVII, Fig. 1; Taylor 1928, p. 170. Børgesen 1916–20, p. 255, Fig. 248–250.

Chondria polyrhiza Collins and Hervey

Mexico: On *Thalassia*, Los Hornos (inner) reef, Vera Cruz.

Collins and Hervey 1917, p. 121, pl. II, Fig. 12; Howe 1920, p. 568; Taylor 1928, p. 212; 1960, p. 617.

Chondria sedifolia Harvey

Mexico: At the landward end of Los Hornos reef, Vera Cruz.

Harvey 1853, p. 19, pl. 18G; Hoyt 1917–18, p. 501, pl. CVIII, Fig. 1–2; Taylor 1928, p. 171, pl. 34, Fig. 11; 1960, p. 615.

Chondria tenuissima (Goodenough and Woodward) C. Agardh

Texas: Occasional on rocks along the sea wall at Rockport.

C. Agardh 1822, p. 352; Harvey 1853, p. 21, pl. 18 F; Hoyt 1917–18, p. 500; Taylor 1928, p. 171, pl. 35, Fig. 3; Funk 1955, p. 139, pl. XXVI, Fig. 1–3.

Acanthophora muscoides (Linnaeus) Bory

Mexico: Breakwater at the north end of Los Hornos reef, Vera Cruz.

Bory 1828, p. 156; Harvey 1853, p. 18; Howe 1920, p. 569; Taylor 1928, p. 165, pl. 26, Fig. 7 and pl. 34, Fig. 9; 1960, p. 619, pl. 72, Fig. 3.

Acanthophora spicifera (Vahl) Børgesen

Texas: On the jetties at Brazos Santiago; on buoys in the harbor and on Diplanthera flats, Port Isabel. Mexico: At virtually all reef stations and *Thalassia* flats from which collections were made along the coast of Vera Cruz.

Børgesen 1910a, p. 201. Fig. 18–19; 1916–20, p. 259, Fig. 253–258; Taylor 1928, p. 165, pl. 26, Fig. 5–6 and pl. 34, Fig. 7; 1960, p. 620, pl. 71, Fig. 3; pl. 72, Fig. 1–2.

Laurencia corallopsis (Montagne) Howe

Mexico: Blanquilla reef, Cabo Rojo, Vera Cruz.

Howe 1918, p. 519; 1920, p. 566; Børgesen 1916–20, p. 253 (as *L. cervicornis* Harvey); Taylor 1928, p. 179, pl. 34, Fig. 5–6; 1960, p. 623.

Laurencia intricata Lamouroux

Texas: Washed ashore on the bay side of Padre Island near Brazos Santiago, Cameron County. Mexico: Giote reef, Anton Lizardo, and at the southwest corner of Isla Sacrificios, Vera Cruz.

Lamouroux 1813, p. 131, pl. 9, Fig. 8–9; Børgesen 1916–20, p. 251, Fig. 241–242 (as *L. implicata* J Agardh) ; Howe 1920, p. 566; Taylor 1928, p. 179, pl. 34, Fig. 8; 1960, p. 626.

Laurencia obtusa (Hudson) Lamouroux

Texas: Occasional on rocks along the sea wall at Rockport. Mexico: Los Hornos reef, Giote reef at Anton Lizardo, Vera Cruz.

Lamouroux 1813, p. 130; Collins and Hervey 1917, p. 119; Børgesen 1916–20, p. 247, Fig. 237–240; Taylor 1928, p. 180, pl. 33, Fig. 3; 1960, p. 626.

Laurencia papillosa (Forsskal) Greville

Mexico: At all the open reef stations along the coast of Vera Cruz.

Greville 1830, p. LII; Collins and Hervey 1917, p. 118; Børgesen 1916–20, p. 246, Fig. 236 (not Fig. 235) ; Howe 1920, p. 566; Taylor 1928, p. 180, pl. 35, Fig. 4; 1960, p. 623, pl. 74, Fig. 2.

Laurencia microcladia Kützing

Mexico: Reef at the south edge of Villa del Mar Balneario.

Kützing 1845–71, 15:22, pl. 60, Fig. b and c; Howe 1920, p. 565; Taylor 1928, p. 179; 1960, p. 627.

Laurencia poitei (Lamouroux) Howe

Texas: On *Thalassia* and loose, Aransas Bay about one mile east of the town of Aransas Pass; in the Laguna Madre east of marker 69 at a depth of 4 feet. Abundant. Mexico: Los Hornos reef and jetty, Vera Cruz.

Howe 1905, p. 583; 1918, p. 518; 1920, p. 566; Collins and Hervey 1917, p. 118; Hoyt 1917–18, p. 497 (as *L. tuberculosa* J. Agardh) ; Børgesen 1916–20, p. 245, Fig. 234; Taylor 1928, p. 181, pl. 34, Fig. 4 and 10; 1960, p. 625.

Summary and Comments

Annotated list of 193 species of marine algae is given as a result of collections made along the coast of the Gulf of Mexico between Rockport, Texas, and the southern part of the State of Vera Cruz, Mexico.

One hundred and sixteen of these species were recorded for Texas, 140 for Mexico. The greater number from Mexico is indicative of a richer flora rather than more thorough collecting. South of the Rio Grande, especially along the coast of Vera Cruz and southward, there is an abundance of favorable substrata (limestone rocks) and warmer inshore water during the winter.

Table 1 is a breakdown of the collections by division and area.

The greater number of Cyanophyta from Texas is believed to be the result of more thorough collecting in the area, especially of the small, inconspicuous species. While a more abundant cyanophycean flora is to be expected along the Texas coast, a greater number of species is to be expected south of the Rio Grande in the more tropical waters and the greater variety of coastal habitats.

In general, the red algae constitute from 45 to 55 per cent of the total flora in areas of the tropical Atlantic where collecting has been reasonably thorough (Collins 1901,

TABLE 1

Species of algae from Texas and Mexico, divided among the four major divisions, and the total collection. The number of species is given for each category and the percentage of the total.

	Texas		Mexico		Totals	
	No. of species	Per cent	No. of species	Per cent	No. of species	Per cent
Cyanophyta	20	17	10	07	24	12
Chlorophyta	27	23	35	25	46	24
Phaeophyta	14	12	25	18	31	16
Rhodophyta	55	48	70	50	92	48
Totals	116		140		193	

p. 296, Table III). Taylor (1928) did not make such an analysis of his Florida records, but the percentages of these are: Cyanophyta 10, Chlorophyta 25, Phaeophyta 13, and Rhodophyta 52 for a total of 400 species.

Probably the percentage of the red algae recorded from Mexico will increase as better knowledge of this group is obtained, but the percentage for Texas may be representative of the flora since collecting in Texas has been more thorough. The lower percentages of Chlorophyta in Texas as compared to Mexico may be ascribed to the many species of tropical Siphonales and Siphonocladiales that do not occur north of the Rio Grande. The greater percentage of browns from Mexico is a result of the abundance of many tropical Dictyotales for which Texas coastal waters are both too cool in winter and lacking in suitable substrata.

The algae listed here represent only a portion of the many collections yet to be studied. As work of identification of the remainder is completed, additions to this list will be published.

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Phytoplankton of the Eastern Mississippi Delta[1]

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Abstract

Phytoplankton samples were obtained from over 100 stations in the eastern Mississippi Delta from June, 1955 through May, 1957. Measurements were also made of chlorinity, temperature, suspended solids, soluble silica, phosphate, and water transparency. Five general areas were surveyed which ranged from fresh water in the Mississippi River to sea water in the open Gulf of Mexico.

The phytoplankton consisted mainly of diatoms, although a few dinoflagellates and other forms were found. Two phytoplankton associations were recognized: a river association containing species of *Melosira, Cyclotella,* and *Navicula,* and a Gulf association consisting of species of *Nitzschia, Thallasiothrix, Thalassionema, Skeletonema, Chaetoceros,* and *Asterionella.* The river population was found mainly in the river, the Gulf population in the Gulf of Mexico. Both populations were mixed in the immediate offshore area. An annotated checklist of all phytoplankton species found in this survey is presented. The phytoplankton populations duirng each field season are described in relation to meteorological and hydrographic conditions.

Maximum populations of phytoplankton were found from January through June in the fresher waters, and in May in the Gulf of Mexico. Minimum populations were found in the fall months. These populations were higher than have been found elsewhere in the Gulf, and more species were encountered. A few comparisons between surface samples and subsurface samples showed that nearly all of the cells were at the surface, except in the river where the water was well mixed.

Introduction

During the period from November, 1954, to July, 1957, seasonal field trips were made to the eastern Mississippi Delta for the purpose of measuring phytoplankton production in the waters of that region (Thomas and Simmons, 1960). Routine measurements of chlorinity, water temperature, pH, turbidity and nutrient concentrations were made also. In this paper the phytoplankton found in this region is indicated, and certain of the environmental conditions associated with the occurrence of these forms are described. A checklist of all forms identified is presented.

Previous Investigations in the Region

Apparently little has been published on the phytoplankton of the delta. Riley (1937) gives chlorophyll values in Harvey units but does not list species or cell numbers. The Zoology Department of Tulane University (1954) has published checklists of the phytoplankton of nearby Lake Pontchartrain but this survey did not extend into delta waters.

Phytoplankton production in the region as measured by the C^{14} method was described by Thomas and Simmons (1960). Surface production was found to equal or

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exceed that of other highly productive tropical or subtropical waters, but was also quite variable, even from day to day. Production at seaward locations was higher during periods of high river discharge than during low water stages. Rough calculations of rates of deposition of organic carbon were compared with phytoplankton production. Some carbon might be contributed to the sediments by phytoplankton at the most seaward locations off the Delta, but very little would be contributed at inshore areas where deposition rates are high.

Description of the Region

The eastern Mississippi Delta (Fig. 1) is dominated by the river which enters into this part of the Gulf of Mexico through Main Pass, Pass-a-Loutre and North Pass. Dozens of smaller channels and drainage ditches are present in the swamps and marshes and these are periodically flushed out into the sea. A few small islands of the Chendeleur chain are located in the northeastern section of the area under consideration.

The river varies in flow, silt load, color and temperature affecting the entire eastern delta. During flood stage (January to June), turbid fresh water extended far into the Gulf, forming plumes of fresh water overlaying more saline water. Near the river these plumes were formed of dark brown fresh water, while further seaward this color was less pronounced and the water was more saline. There was frequently a sharp line of demarcation between the two colors and where this was seen there were over 200 mg/l suspended solids in the darker water and less than 100 mg/l in the lighter. Scruton and Moore (1953) indicated that the sand, silt, and clay components of suspended solids settle out at different rates causing differently colored waters. In a few instances an area of still lighter water was observed, but there was no drastic change in suspended solids. For descriptive purposes the waters of darker color containing more than 200 mg/l suspended solids are termed "primary" plumes while the lighter colored waters containing fewer suspended solids are termed "secondary" plumes.

In February, 1956–1957, tides were low and these plumes were very widespread. In May, 1957, high tides restricted the plumes and there was movement of this fresh water parallel to the shore. During the summer and fall the river was low and less turbid, and a salt wedge extended well into the stream.

Water temperature varied from 8.0°C in the river in February, 1956, to 28.0°C in the Gulf in October, 1956, and probably was even higher in July and August. Chlorinity ranged from 0.04 to 19.00 ‰ in the areas investigated.

Five general areas were included in the survey (Fig. 1). Area 1, the river, was characterized by deep channels and chlorinity normally below 1.00 ‰. Area 2, the primary plume, had, during the flood season, over 200 mg/l suspended solids and a chlorinity range of 0.04–6.00 ‰. Area 3, the Gulf beyond the primary plume, had chlorinity above 10.0 ‰, was fairly clear (Secchi disc observed 1–7 meters), and was probably the zone where nutrients from the river were utilized by the phytoplankton. Area 4, Breton Sound, had chlorinities similar to Area 3 but had less wave action and currents from the Gulf. Area 5, Blind Bay, was a shallow bay connected to both the Gulf and the river and was subject to wide ranges in chlorinity and temperature.

More detailed descriptions of the region may be found in papers by Shaw (1913), Shepard (1954), Scruton and Moore (1953), Scruton (1956), and Parker (1956).

The supply of nutrients to the phytoplankton has been described in a previous paper

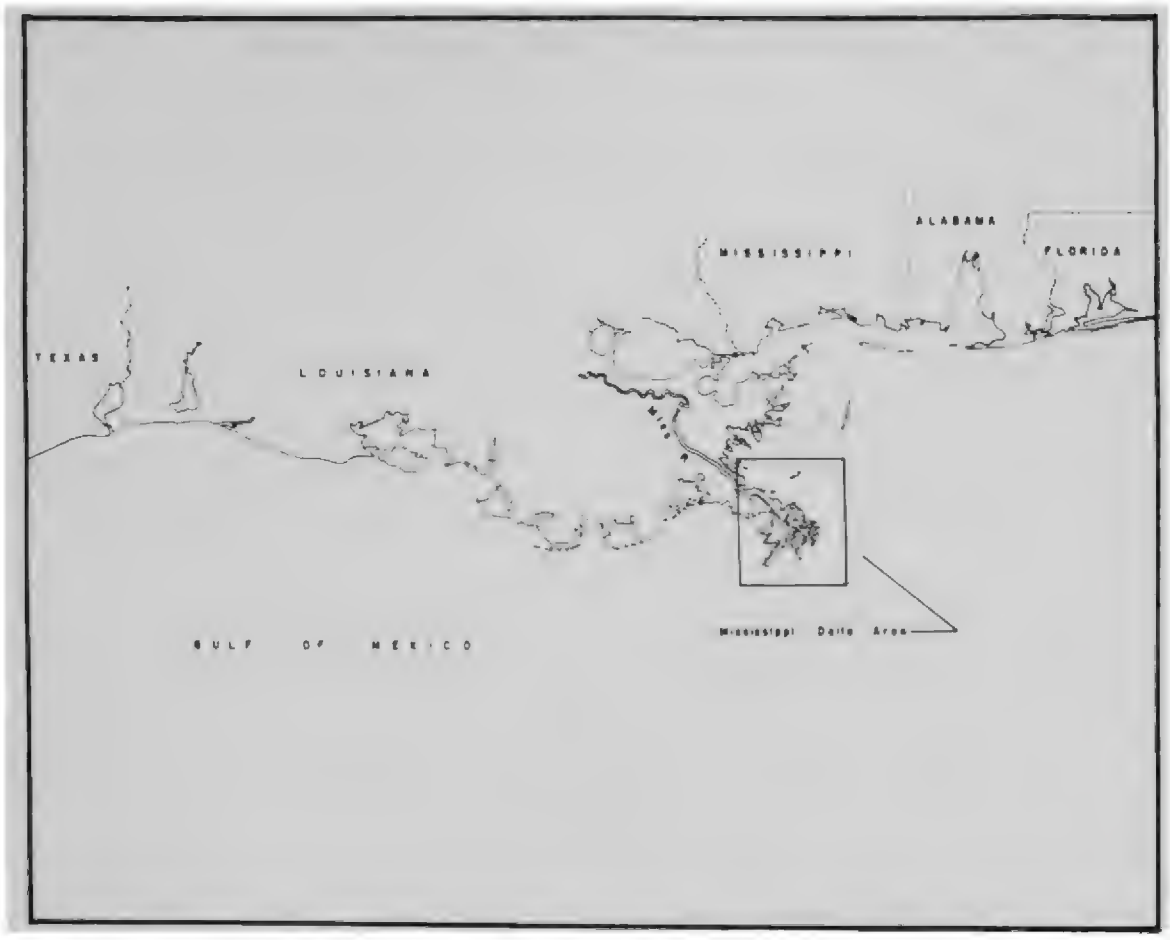

FIG. 1. Maps of the study area. a. Northern Gulf of Mexico showing the Mississippi Delta area within the square. b. Enlarged map of the Mississippi Delta inset.

(Thomas and Simmons, 1960). Phosphate was seldom a limiting factor in these waters, a conclusion which agrees with that of Riley (1937). During times of high water (February through May), there were no significant differences in inorganic phosphate concentration between the river, the primary plume, or the Gulf (Thomas and Simmons, 1960). In the fall months, however, the phosphate concentration in the Gulf was significantly lower than that of the river and plume. The phosphate concentration in the plume did not change significantly from season to season, but in the Gulf beyond the plume, significantly more phosphate was found during May than in the fall months.

More detailed distributions of phosphate were obtained during seaward traverses made on single days in February and May, 1957. These showed that there was an increase in phosphate toward the edge of the primary plume followed by a decrease further seaward. This increase may have resulted from an interaction (or exchange) between anions in the seawater and phosphate contained in suspended matter. Similarly, high phosphate in the plume (3.72–4.07 μg/at./L) in September, 1956, may have been released from sediments as saline water of the high incoming tides passed over them. Such processes were described by Rochford (1951) for some Australian estuaries.

The nitrogen supply estimated from analyses of the combined Kjeldahl and ammonia fraction is reported by Thomas and Simmons (1960). The nitrate analyses used were not reliable. At any one season no significant differences in nitrogen were found from one area to another. The Gulf water contained significantly more Kjeldahl- and ammonia-nitrogen in May than in the fall months. In this respect, the distribution was similar to that of phosphate.

The distribution of soluble silica in these waters was described by Bien, Contois, and Thomas (1958). They showed that silica was removed from fresh water as it mixed with sea water. Part of this removal was due to chemical interaction between soluble silica, suspended matter, and electrolytes in sea water. An additional portion was probably taken up by diatoms. At offshore stations, only traces of soluble silica were found, and silica may have been limiting at these locations.

Methods

Inorganic phosphorus. Samples were collected in 60 ml polyethylene bottles and were kept frozen with dry ice. They were analyzed by the method of Wooster and Rakestraw (1951) at a later date, but were not corrected for salt error.

Dissolved silicates. Samples were collected in 60 ml polyethylene bottles and analyzed by the method of Dienert and Wandenbulke (1923) and were corrected for salt error.

Chlorinity. Samples were collected in 60 ml bottles and their chlorinity determined by Mohr titration with an accuracy of 0.02 ‰.

Temperature. Readings accurate to 0.2 degrees centigrade, were taken with a bucket thermometer at the surface and from aliquot of a Van Dorn sampler at depths.

Turbidity and total suspended solids. Secchi discs were used during some trips; at other times samples were Millipore-filtered and the total suspended solids determined gravimetrically.

Phytoplankton collecting. Samples were collected in 60 ml polyethylene bottles and preserved with 1.5 ml of 100 per cent neutralized formalin or with Lugol's iodine. Duplicate samples were frequently taken.

Phytoplankton fixation. Slides were prepared using the Millipore-filter method de-

scriped by Holmes and Reid (in press). A 10 ml aliquot of the samples was filtered through a gridded HA Millipore filter (0.4 to 0.6 μ pore size) using a vacuum of 10–12 psi. Higher vacuum distorted the plankton. The filter was then washed successively with small quantities of 75, 50, 25, and 10 per cent millipore-filtered sea water; with distilled water; then with 10, 25, 50, 70, 95, and 100 per cent ethanol. A one per cent solution of Fast Green stain was then allowed to stand on the filter for 10 minutes or until the cells were distinctly colored. The filter was then placed on a drop of beechwood creosote on a 50 x 75 mm glass slide and allowed to clear. Canada Balsam was applied and a cover-slip placed over the filter. After gentle heat was applied for 12–24 hours, the slide was ready for counting.

Modifications of this method were used occasionally. In extremely muddy water only two ml of the sample were filtered; in samples with sparse populations a 100 ml aliquot was used. Methanol was sometimes substituted for ethanol but did not work as well and various other strains were used, none of which were superior to Fast Green.

This method enables the investigator to prepare slides quickly and to examine fairly large aliquots rapidly. It retains small species and there is no problem of clogging or overflowing of nets. However, most flagellates are destroyed when this method is used.

Cells were not counted and reported unless green plastids were observed. No obviously dead cells were included.

Phytoplankton counting. During the early part of the survey, counting proceeded until 50 individuals of any species had been listed. Later, all of the larger forms on the slide were counted at low magnifications; then 10 per cent of the slide was examined under higher powers and all forms on this portion were counted. Some slides were re-examined several months after the first count and the cell number agreed within 10 per cent. Aliquot from duplicate bottles taken at the same station agreed within 15 per cent, and duplicate slides from the same sample agreed within 10 per cent.

The area either contained few flagellates, blue-green, and green algae, or these forms were not preserved. No significant differences were observed in samples fixed with formalin and those with Lugol's iodine. No flagellates were found in quick frozen net samples. Diatoms kept very well and, for net samples, this method may be superior to the use of chemical preservation.

Identification of the phytoplankton was aided by the monographs of Smith (1933), Cupp (1943), Hustedt (1930 *et seq.*), and Schiller (1933 *et seq.*).

All of the data, upon which the ensuing discussion is based, have been compiled into a set of tables, one table for each station. These can be made available to interested persons upon request.

Areas Sampled

Samples were collected from 138 stations during this survey. Some of these were occupied on two or more consecutive days and samples were taken at various depths in a few cases. In June, 1955, one station in the river, four in the Gulf and two at Breton Island were occupied. In October, 1955, sampling was more intense and there was one station in the river, two in plume, four in the Gulf, two in Breton Sound, and three in Blind Bay. The river was very high in February, 1956, and two stations were occupied in the river, one in the plume, two in Breton Sound, and one in Blind Bay. During the low water period in September, 1956, one station was occupied in the river, three in the

Gulf, three in Breton Sound, and one in Blind Bay. In November, 1956, the river was low, as was the tide. Sampling was done at two points in the river, 14 in the Gulf and one in Breton Sound. High water in February, 1957, restricted most sampling to the river, but five stations were also occupied in the plume, two in the Gulf and two in Blind Bay. During the May, 1957, trip 35 stations were sampled. There were 24 in the Gulf, 10 in the plume and one in the river. Stations sampled prior to June, 1955, are not included since data are limited.

Net tows were made in the Gulf in May, 1957, at stations about five miles northwest of Breton Island.

Annotated Checklist of the Phytoplankton of the Eastern Mississippi Delta

The method used by Conover (1956) for separating major species from minor ones was adapted for use in the delta. The chief difference in the methods is that some species which were present at all seasons were considered major constituents even if the cell concentration was never more than five per cent of the total phytoplankton. A few species which appeared in numbers greater than five per cent of the total were not considered of major importance because they appeared sporadically. Table 1 lists the major species by season and by cell concentration. Minor species are shown in Table 2. Certain of these are discussed below in more detail.

Melosira. The species of the genus *Melosira* comprise one of the most important groups of diatoms found in the eastern Mississippi Delta. *Melosira granulata,* a fresh water species, was normally most abundant in the river and primary plume during flood seasons. When high concentrations were found, the chlorinity was normally less than 0.14 ‰, and the water temperature ranged from 8.0° to 20.0°C. Some of these cells contained chloroplasts but many appeared to be in poor condition. Somewhat less robust cells, resembling *M. granulata* var *angustissima* Muller, were often found associated with *Melosira granulata. Melosira distans*, a fresh water species of ponds and ditches, was found in nearly fresh water and in salt water. In November, 1956, no cells of *Melosira* were found. *Melosira sulcata* (Ehrenberg) Kutzing was never abundant but did replace others of the genus in the Gulf.

Skeletonema costatum (Greville) Cleve was fairly abundant in all areas outside the plume during the period from February to June. One general bloom of phytoplankton was observed near Breton Island in February, 1956. The cell concentration of *Skeletonema costatum* was 14,311/ml.

Cyclotella. The listing of the entire genus as *Cyclotella sp.* in early counts complicates the analysis of the group.

Cyclotella comta (Ehrenberg) Kutzing, planktonic in lotic and lentic fresh water environments, and *C. meneghingiana* Kutzing, a salt-tolerant littoral species, were present whenever fresh water forms of *Melosira* were encountered. Concentrations of *C. meneghingiana* were noted in the river and plume in chlorinites of 0.04–0.13 ‰ in February, 1957. Concentrations of *C. comta* were very similar in these instances. In May, 1957, Blind Bay had almost identical chlorinity and similar cell concentrations. *C. caspia* Grunow was encountered at Breton Sound in September, 1956, at a chlorinity of 15.14 ‰. The cell concentration was 4,200/ml. *C. operculata* (Agardh)

TABLE 1

Cells per milliliter of major phytoplankton species in the eastern Mississippi Delta, June, 1955 to May, 1957*

Species	Area	June 1955	October 1955	February 1956	September 1956	November 1956	February 1957	May 1957
Melosira granulata (Ehrenberg) Ralfs	1	203	49	1798	100	0	765–1089	1315
	2	.....	0	224	.....	.....	410–1640	23–330
	3	117	0	.....	32	60	.....	35
	5	.....	0	1021	100	.....	1355–2862	.....
M. distans (Ehrenberg) Ralfs	1	0	0	912	0	0	810–1116	880
	2	.....	0	0	.....	.....	117–2120	180–615
	3	0	0	.....	38–240	0	.....	100–1000
	5	.....	0	0	0	.....	1200–2550	.....
M. sulcata (Ehrenberg) Kutzing	1	0	0	226	0	0	0	0
	2	.....	0	597	.....	.....	0	35
	3	0	0	.....	10	0	.....	35
Skeletonema costatum (Greville) Cleve	3	0	0	.....	0	0	.....	25–235
	4	0	0	14,311	0	0	.....	.....
Cyclotella spp.	1	124	50	400	0	0	0	10
	2	471	21–76	452	0	.....	60–95	1–35
	3	21–1284	0	.....	0	30	.....	2–70
	4	119–147	0	876–1527	0	0	.....	.....
	5	.....	0	1888–4552	0	.....	200	.....
C. comta (Ehrenberg) Kutzing	1	0	0	0	800	0	135–270	200
	2	.....	0	0	.....	.....	40–230	1–60
	5	.....	0	0	0	.....	25	.....
C. meneghingiana Kutzing	1	0	0	0	40	0	135–270	210
	2	.....	0	8–35	.....	.....	120–230	1–45
	3	0	0	.....	0	0	.....	1–3260
	4	0	0	0	8–35	0	.....	.....
	5	.....	0	.....	40	.....	170–358	.....

TABLE 1—Continued

Cells per milliliter of major phytoplankton species in the eastern Mississippi Delta, June, 1955 to May, 1957*

Species	Area	June 1955	October 1955	February 1956	September 1956	November 1956	February 1957	May 1957
C. caspia Grunow	4	0	0	0	4200	0	.....	.....
C. operculata (Agardh) Kutzing	5	.....	0	0	60	.....	200–250	.....
Coscinodiscus spp. Ehrenberg	1	0	6	791	0	3	1	2
	2	.....	210	23	.....	.....	0	+
	3	3	6–29	.....	60	0	.....	+–8
	4	0	37–51	0	0	0	.....	.....
	5	.....	+	278	0	.....	0	.....
C. excentricus Ehrenberg	2	.....	0	0	.....	0	0	0
C. nitidus Gregory	2	.....	0	60	50	.....	0–5	+–20
	3	0	0	.....	0	10	.....	+–20
	5	.....	0	0	0	.....	.....	.....
Chaetoceros spp. Ehrenberg	2	.....	0	90	.....	.....	+–50	35–50
	3	8	5–86	.....	0	0	.....	5–134
	4	274	9–100	0	0	0	.....	.....
C. lorenzianus Grunow	2	.....	0	135	.....	.....	0	0
	3	0	20	.....	0	0	.....	7–45
C. compressus Lauder	4	118–177	0	0	0	0	.....	.....
C. didymus Ehrenberg	3	18–24	0	.....	0	0	.....	0
	4	0	+	254	0	0	.....	.....
C. affinis Lauder	2	.....	0	88	.....	.....	1–20	1–60
	3	423	0	.....	0	0	.....	70–182
	4	147–650	0	982	8	0	.....	.....
C. costatus Pauillard	2	.....	0	23	.....	.....	0	0
	4	0	0	675	0	0	.....	.....
C. pelagicus Cleve	2	.....	0	22	.....	.....	0	0
	3	0	0	0	0	0	.....	10–140
C. brevis Schutt	3	0	0	.....	0	0	.....	1–35

TABLE 1—Continued

Cells per milliliter of major phytoplankton species in the eastern Mississippi Delta, June, 1955 to May, 1957*

Species	Area	June 1955	October 1955	February 1956	September 1956	November 1956	February 1957	May 1957
C. diversus Cleve	2	.....	0	+	.....	.....	0	1–10
	3	0	12–56	.....	0	0	0	10–182
	4	43	55	0	2	0	.....	.....
Diatoma spp. de Candolle	2	.....	0	0	.....	.....	+–40	1–50
D. vulgare Bory	3	0	133	.....	0	0	.....	0–0
D. hemale (Lyngbye) Heiberg	4	0	0–5	0	30	0	.....	.....
	5	.....	0	0	0	.....	+–80	.....
Eunotia sp. Ehrenberg	3	0	0	.....	+	0	.....	+–1000
Plagiogramma vanheurkii Grunow	2	.....	0	0	.....	.....	10–90	1–20
	3	0	1	.....	0	0	.....	+–63
Thalassionema nitzschioides Grunow	2	.....	6	0	.....	.....	4–100	10–40
	3	+	153–282	.....	+	20	.....	6–96
	4	+	0	20	55	0	.....	.....
Thalassiothrix frauenfeldii Grunow	1	0	0	0	0	0	0	5
	2	.....	0	22	.....	.....	0–5	5–23
	3	0	6–570	.....	0	0	.....	6–84
Asterionella japonica Cleve	2	.....	0	0	.....	.....	1–50	15–98
	3	47	24–84	.....	0	6–20	.....	40–377
	4	368	0	3135	2–10	0	.....	.....
A. formosa Cleve	1	0	—+	0	0	50	0–40	1–12
A. gracillima (Hantzschel) Heiberg	2	.....	+	+	.....	.....	2–125	0
	5	.....	0	0	+	10	5–120	.....
Achnanthes sp. Bory	2	.....	0	0	.....	.....	0	3–10
	3	0	0	.....	0	0	0	1–20
	4	0	0	0	85	0	.....	.....
	5	.....	0	0	20	.....	42–50	.....
Navicula spp. Bory	2	.....	0	0	.....	.....	0	3–10
	3	0	7–15	.....	0	2	.....	1–10
	4	+	34–74	99	20	0	0	.....
	5	.....	11–93	0	0	.....	0–10	.....

TABLE 1—Continued

Cells per milliliter of major phytoplankton species in the eastern Mississippi Delta, June, 1955 to May, 1957*

Species	Area	June 1955	October 1955	February 1956	September 1956	November 1956	February 1957	May 1957
N. distans (W. Smith) Ralfs	1	0	0	0	0	0	1–24	0
	2	.....	0	0	.....	.....	7–18	1–10
	3	0	0	.....	0	50	0	1–10
N. gracilis Ehrenberg	1	0	0	0	0	0	24–53	0
	2	.....	0	0	.....	.....	6–164	1–40
	5	.....	0	0	0	.....	18–63	.....
N. rhyncocephala Kutzing	1	0	0	0	0	0	30–50	+
	2	.....	0	0	.....	.....	10–25	0
Gyrosigma sp. Hassall	1	0	0	0	0	0	1–5	0
	2	.....	0	0	.....	.....	1–40	+
	3	0	3	.....	0	60	0	1–5
	4	0	0	79	0	0	.....	.....
	5	.....	229–619	0	20	.....	+	.....
Nitzschia sp. Hassall	2	.....	0	0	0	.....	0–25	0
	4	231	0	99	0	0	.....	.....
N. bilobata var *minor* Grunow	2	.....	0	0	.....	.....	0	0–5
	3	0	18	.....	0	0	.....	3–48
	5	.....	0	0	40	.....	0	0
Nitzschia closterium (Ehrenberg) W. Smith	2	.....	35	23	.....	.....	0	0
	3	0	47–74	.....	0	0	.....	3–70
	4	0	94	139	0	0	.....	.....
	5	.....	98–490	0	0	.....	0	.....
N. longissima (Brebisson) Ralfs	2	0	0	0	.....	.....	18–270	5–10
	3	0	0	.....	.....	0	.....	20–40
	4	0	6	+	30	0	.....	.....
Nitzschia seriata Cleve	1	0	0	0	0	0	0–18	0
	2	.....	12	23	.....	.....	0–8	0–15
	3	0	17–187	.....	0	0	.....	6–66
	4	235–247	55	20	0	0	.....	.....
Scenedesmus sp. Meyen	2	.....	82–131	0	.....	.....	0	0
Chilomonas marina	2	.....	6–100	0	.....	.....	0	0
	3	0	3–33	.....	0	0	.....	0
	4	235–247	55	20	0	0	.....	.....

* Note: "0" indicates that area was sampled but no cells of the species were found. "....." indicates that area was not sampled during that season. "+" indicates that cells were present in concentrations of less than 1/ml.

TABLE 2

Minor phytoplankton species of the eastern Mississippi Delta

Species	Seasons	Areas found, Cl. ‰
Melosira moniliformis (Muller) Agardh	February, May	Plume
M. islandica O. Muller	February, May	Plume
M. ambigua (Grunow) Muller	February, May	Plume, 1.54–2.92
Stephanopyxis palmeriana (Greville) Grunow	May, November	Gulf
S. turris (Greville and Arnott) Ralfs		
Coscinosira polychorda Gran	October	Plume
Thalassiosira rotula Muenier	May	Gulf
T. decipiens (Grunow) Jorgensen		
Cyclotella antiqua W. Smith	September	Plume
C. bodanica Eulenstein	September, May	Plume, Blind Bay
Coscinodiscus lineatus Grunow	May	Gulf
C. curvisettus Grunow	February, May	Plume, Gulf
C. marginatus Ehrenberg	February, May September, November	Gulf, 14.0–17.0
C. granii Cough		
C. concinnus W. Smith		
C. centralis Ehrenberg		
C. oculus iridis Ehrenberg	February, May September, November	Gulf, 14.0–17.0
Actinoptychus undulatus (Bailey) Ralfs	May	Gulf
A. splendens (Shadbolt) Ralfs	All	Gulf, Breton Sound
Asteromphalus heptactis (Brebisson) Ralfs	February, September	Gulf
Lauderia borealis Gran	May	Gulf
Schroderella delicatula (H. Peragallo)	May	Gulf
Leptocylinderus danicus Cleve	May	Gulf
Guinardia flaccida (Castercane) H. Peragallo	May	Gulf
Rhizosolenia stolterforthi H. Peragallo	February	Gulf near Plume

TABLE 2—Continued

Minor phytoplankton species of the eastern Mississippi Delta

Species	Seasons	Areas found, Cl. ‰
R. robusta Norman		
R. imbricata Brightwell	May, 1957	
R. styliformis Brightwell	net samples	
R. calcar avis M. Schultze		
R. alata Brightwell		
R. acuminata (H. Peragallo) Gran		
R. setigerra Brightwell	February, May, October	Gulf, 13.0–19.0
Bacteriastrum delicatulum Cleve	October	Gulf
B. hyalinum Lauder	May	Gulf
B. cumosum Pauillard		
Chaetoceros concavicornis Mangin	May	Gulf, net sample
C. van Heurkii Gran	May	Gulf
C. decipiens Cleve	May	Plume, Gulf
C. convolutus Castercane	September	Gulf
C. peruvianus Brightwell	May, September	Gulf, Breton Sound
C. decipiens form *singularis* Gran	May	Gulf
C. teres Cleve	May	Gulf
C. constrictus Gran	May	Gulf
C. affinis var *willei* (Gran) Hustedt	May	Gulf
C. lacinosus Schutt	February, May	Breton Sound, Gulf
C. laevis Leuduger-Fortmorel	May	Gulf
C. messanensis Castercane	June 1955	Gulf
C. similis Cleve	May 1957	Gulf
C. curvisettus Cleve	February 1956 May 1957	Breton Sound Gulf
C. pseudocurvisettus Mangin	February 1956–1957	Breton Sound, Plume
C. socialis Lauder	February, May	Plume, Breton Sound
C. gracillis Schutt	May 1957	Gulf

TABLE 2—Continued

Minor phytoplankton species of the eastern Mississippi Delta

Species	Seasons	Areas found, Cl. ‰
C. vistulae Apstein	May 1957	Gulf
Eucampia cornuta (Cleve) Grunow	May net samples	Gulf
Ditylum brightwellii (West) Grunow	May net samples October 1955	Gulf Breton Sound
Lithodesmium undulatum Ehrenberg	February 1956	Breton Sound
Triceratium broeckii Leuduger-Fortmorel	February 1957	Plume, near Breton Island
Bidulphia mobiliensis Bailey	October, February, May	Gulf, Breton Sound, 10.0–16.0
B. aurita (Lyngbye) Brebisson and Godey	November, February, May	Plume, Gulf, Breton Sound
B. rhombus (Ehrenberg) W. Smith	February 1956	Breton Sound
B. dubia (Brightwell) Cleve	February 1956, May	Plume, Gulf
Hemiaulus hauchii Grunow	All seasons	Plume, Gulf, Breton Sound
Tabellarii sp. Ehrenberg	February 1957	Blind Bay, 0.4
T. fenestrata (Lyngbye) Kutzing	May 1957	Gulf
T. fenestrata var. *asterionelloides* Grunow	May 1957	Gulf
Diatoma elongatum Agardh	February 1957	River
Striatella delicatula (Kutzing) Grunow	May 1957	Gulf
Grammatophora marina Ehrenberg	February, May, September	Gulf, near river
G. oceanica (Ehrenberg) Grunow	May 1957	Gulf net samples
Licmophora abbreviata Agardh	May 1957	Plume
Climacosphenia moniligera Ehrenberg	May 1957	Gulf net samples
Campylosira cymbelliformis (A. Schmidt) Grunow	February 1957	Plume
Fragilaria sp. Lyngbye	February, May, September	All areas, 0–19.0
F. crotonensis Kitton	February, May, September	All areas, 0–19.0
Synedra sp. Bailey	February, May	Plume, river, 0–7.0
S. ulna (Nitzsch) Ehrenberg	May 1957	Gulf net samples
S. actinastroides Lemmerman	May, September	Gulf, near plume
Thallassiothrix longissima Cleve and Grunow	May, November	Gulf, near Main Pass

TABLE 2—Continued

Minor phytoplankton species of the eastern Mississippi Delta

Species	Seasons	Areas found, Cl. ‰
T. mediterranea var. *Pacifica* Cupp	All seasons (May)	Gulf
T. delicatula Cupp	February, 1956–57 May	Gulf, near plume
Pseudoeunotia Grunow	May 1957	Plume, near river
P. doliolus (Wallich) Grunow		
Cocconeis sp. (Ehrenberg)	May, September, October	Gulf
C. diminuta	September 1956	Gulf, near Pass-a-Loutre
C. placentula (Ehrenberg)	February 1957	Plume
Navicula membranacea Cleve	May 1957	Gulf net samples
N. simplex Krackbe	May 1957	Plume
Gyrosigma spencerii (Quekett) Cleve	February 1957	Plume
Pleurosigma sp. W. Smith	February, May	River, Gulf
P. normanii Ralfs	February 1957, May	Plume, Gulf
P. elongatum W. Smith	February 1957, May	Plume, Gulf
Caloneis sp. Cleve	May 1957	River, 0–0.6
Nedium affine Pfitzer	February, September	River, Blind Bay, 0–2.0
Diploneis sp. Ehrenberg	All seasons	River, Plume
D. interrupta (Kutzing) Cleve	February 1957	Plume
Stauroneis anceps Ehrenberg	February, May, September	River, Plume, 0–6.0
Amphipleura sp. Kutzing	February 1956	River, 0–0.8
Pinnularia sp. Ehrenberg	February 1957	Plume
P. viridis (Nitzschia) Ehrenberg		
Amphiphora gigantea var. *sulcata* (O'Meara) Cleve	May 1957	Plume
Comphonema vibra Agardh	February 1957	River, 0–0.8
Cymbella sp. Agardh	February 1957, May	River
C. lanceolata	February 1957, May	River
Ephithemia sp. de Bribisson	February 1957, May	River
E. zebra (Ehrenberg) Kutzing	February 1957, May	Plume, Blind Bay
Nitzschia pungens var. *Atlantica* Cleve	May 1957	Plume

TABLE 2—Continued

Minor phytoplankton species of the eastern Mississippi Delta

Species	Seasons	Areas found, Cl. ‰
N. pacifica Cupp	May 1957	Plume
N. palea (Kutzing) W. Smith	May 1957	Plume
N. paradoxa (Gmelin) Grunow	February 1956–1957	Plume
Surirella sp. Turpin	February, 1957 May	Plume, Gulf
S. fastuosa var. *recedens*	May 1957	Plume
	Other phytoplankton	
Chroococcus sp. Nageli	February 1956	River, 0–0.8
Lyngbye sp.	October 1955	Gulf
Nostoc sp. Vaucher	October 1955, February 1956–57	River, Plume
Cylindroscapsa sp. Reinsch	October 1955	Gulf
Tetrastrum sp. Chodat	October 1955	River
Actinastrum hantzschii Lagerheim	February 1956	River
Ceratium sp. Schrank		
C. furca (Ehrenberg) Claparede and Lachmann		
C. tripos (O. F. Muller) Nitzsch		
C. fusus (Ehrenberg) Dujardin	June, October, 1955	Gulf, Breton Sound
Glenodinium sp. Kelbs	October 1955, May	Gulf
Goniodoma sp. Stein	June, October	Widespread in Gulf, nowhere abundant
Pyrocystis Murray	June, October	Widespread in Gulf, nowhere abundant
P. pseudonoctoluca (W. Thompson)	June, October	Widespread in Gulf, nowhere abundant
Hypodinium sphericum Kelbs	June, October	Widespread in Gulf, nowhere abundant
Gymnodinium sp. Stein	June, October	Widespread in Gulf, nowhere abundant
Gloedinium sp. Kelbs	June, October	Widespread in Gulf, nowhere abundant
Peridinium sp. Ehrenberg	June, October	Widespread in Gulf, nowhere abundant
Hemidinium sp. Stein	June, October	Widespread in Gulf, nowhere abundant
Dinophysis sp. Ehrenberg	June, October	Widespread in Gulf, nowhere abundant
D. caudata Saville-Kent	June, October	Widespread in Gulf, nowhere abundant
Euglenopsis vivax Kelbs	February 1957	River (from marshes)

Kutzing was present in samples taken in September at Blind Bay and in February, 1957, in the plume. However, the heaviest population discovered, containing 1,490 cells/ml, was taken in the plume near Pass-a-Loutre in May, 1957. This genus was often found together with *C. meneghingiana* and idtentification was usually difficult.

Coscinodiscus excentricus Ehrenberg was abundant in September, 1956, in Breton Sound. The chlorinity was 18.37 ‰ and the water temperature was 25.8°C. *C. nitidus* Gregory was most abundant in the Gulf in November, 1956.

Chaetoceros. The genus *Chaetoceros* was widespread in the delta and 26 species were identified. Only two oceanic forms are included in this group, the remainder being neritic. None were found at chlorinities less than 7.00 ‰ and, in general, the cnocentrations were maximum in May, 1957, and June, 1955. There were also sizable populations in October, 1955, in the Gulf.

C. lorenzianus Grunow, a tropical and temperate species (Cupp, 1943), was found in February, 1956 and in May, 1957, at several Gulf stations. One small concentration was encountered in October, 1955, in the Gulf.

C. compressus Lauder was found only in the June, 1955, samples near Breton Island. The chlorinity was 12.35–15.24 ‰ and the water temperature was 23.6°C. Conover (1956) reported this species for all seasons in Long Island Sound with a spring flowering in May, 1953, and a peak in August, 1952. Her data indicate that low light intensity and high nutrient concentrations were necessary for this form. These conditions were met in May in the delta. Cupp and Allen (1938) list this as a very important species in the Gulf of California in March, June, November and December.

C. affinis Lauder was one of the most abundant representatives of the genus in February, 1956, May, 1957, and June, 1955. It was found in the Gulf at chlorinities of 14.0–17.0 ‰. Conover (1956) observed this species more often at offshore stations than at inshore stations in Long Island Sound but found the higher concentrations in August and September. Cupp (1943) lists this species as numerous from May through August off California. In the Mississippi Delta its peak of abundance coincides with the flood period.

C. pelagicus Cleve was another species found in May, 1957, at offshore stations. Water temperature was 22.0°C and chlorinity was 14.00–17.00 ‰. Conover's (1956) experimental data suggest that it grows well in moderate light conditions if inorganic nutrients are present.

C. diversus Cleve is a tropical and sub tropical species that was found in the Gulf in all seasons but was most abundant in May. The concentration dropped sharply in June and there was a minor peak in October.

Eunotia Ehrenberg was probably washed in from fresh water, since most species of this genera are calciphobic (personal communication from Dr. R. Patrick) and since it was found only in February, 1957, and May, 1957, during floodstage.

Thalassionema nitzschioides Grunow, a north temperate species, was abundant in the delta. There were two widely separated peaks of abundance with the major one in October, 1955, and a minor one in May, 1957. At stations where the concentration was high, chlorinity ranged from 13.25 to 17.14 ‰. These peaks are different from those reported by Cupp and Allen (1938).

Thalassiothrix frauenfeldii Grunow was found everywhere in May, 1957, except in the river and in Blind Bay constituting an important part of the diatom flora. It was

found at only two stations in September, 1956, and October, 1955, and isolated patches also were found in November, 1956, February, 1956, and February, 1957. This species was reported to be abundant in August, 1926, off southern California by Allen (1938). Sampling was not sufficient to tell if a double peak actually existed or if the dense isolated populations found in September and October were usual.

Asterionella japonica Cleve, a widespread neritic species, in May, 1957, was present at all Gulf stations and was most abundant at a chlorinity range of 10.00–17.00 ‰. In February, 1956, over 3,000 cells/ml were present in a bloom in Breton Sound, but it was not noted in other areas. The species was less abundant in October, 1955, and a few were found in November. In the delta this is apparently a late spring form with an elongated major peak from February to June in Gulf waters. There is apparently a shorter period of flowering in late fall.

A. formosa Cleve and *A. gracillima* (Hantzschel) Beiberg, although never very numerous, were often found in the river and in areas of fresh water near the Gulf. They were most abundant during periods when the river was not at flood stage.

Achnanthes. At least four species of the genus *Achnanthes* Bory were present in the delta (*A. longpipes, A. microcephala, A. depressus* and *A. speciosa*). Because of the difficulty of obtaining accurate identification these are summarized together. The greatest concentration found was in Blind Bay and the plume in February, 1957. The genus was more widespread in May, 1957, than in February but cell numbers were less. Scattered patches were found in September, 1956, and November, 1956.

Navicula. At least a few cells of the genus *Navicula* were found in almost every sample taken in the eastern Mississippi Delta. *N. rhyncocephala* Kutzing was found only in the primary plume or in fresh water. *N. gracilis* Ehrenberg was similarly distributed except that it was taken in chlorinites as high as 6.00 ‰. *N. distans* (W. Smith) Ralfs was found in fresh water in May, 1957, and was present at nearshore stations throughout the year, being most abundant at chlorinities of 5.00–12.00 ‰.

Gyrosigma. Species of the genus *Gyrosigma* Hassall were found in every season except June, 1955. However, the only times it assumed a position of importance were in October, 1955, in Blind Bay, and in February, 1957, in Breton Sound. In the latter case, *G. balticum* was the species present.

Nitzschia. Some species of the genus *Nitzschia* Hassall were present in every season except November, 1956. The most dense populations identified only to genus were found in the Gulf off Pass-a-Loutre in June, 1955, and in February, 1957. *N. bilobata* var *minor* Grunow was present at chlorinities ranging from 1.92 to 17.14 ‰. *N. closterium* (Ehrenberg) W. Smith was taken in October, 1955; February, 1956; and May, 1957, and was widespread in October and May. Highest cell concentrations were found in areas of moderate chlorinity (4.00–12.00 ‰) and at stations near the plume or river.

N. longissima (Brebisson) Ralfs was found in February, May, September and October, but was abundant only in the Gulf in February, 1957. The chlorinity tolerance was great (1.00–18.00 ‰) but highest cell numbers were found near the plume. Conover (1956) found that high temperature, moderate to high light intensity and enriched water seemed favorable for growth of this species. Most of these conditions are met just outside the plume.

N. seriata Cleve was widespread in the area and was most numerous in May, 1957,

June, 1955, and in October. Smaller numbers were found in February, 1956, and 1957 and none were taken in September or November. This species was most abundant at chlorinities above 13.00 ‰ and at temperatures of 20.0–23.0°C.

Discussion

Phytoplankton Populations During Each Field Trip in Relation to Hydrographical and Meteorological Conditions

The five general areas varied considerably from each other and there were pronounced seasonal differences in phytoplankton populations. These are shown in Table 3 together with other data on nutrients and physical factors.

In June, 1955, the river was turbid although the peak of the flood season was past. In the river and the barely detectable plume most diatoms were of the genera *Melosira* and *Cyclotella*. In the Gulf and in Breton Sound *Skeletonema costatum* and *Cheatoceros spp.* were abundant.

In October, 1955, the river was low and clear. Phytoplankton was sparse in this area and composed of the *Melosira-Cyclotella* complex. In the Gulf and at Breton Island most of the genera were marine but populations were extremely variable from station to station and on successive days. *Thalassionema nitzschioides* and *Skeletonema costatum* were abundant at most stations.

In February, 1956, with the river at flood stage, swift and turbid, the primary plume extended far into the Gulf. Cell numbers were high throughout the river and the *Melosira-Cyclotella* complex was very evident. Near Breton Island a "pulse" of diatoms occurred with *Skeletonema costatum* as the major species.

During September, 1956, the river was low and clear and the plume was not pronounced. Chlorinity was fairly high, even in the river. Various species of *Coscinodiscus* were abundant in Breton Sound, species of *Melosira* and *Cyclotella* were common in the river and Blind Bay, and samples from the plume area varied, on successive days, from purely marine to fresh water forms. A "pulse" of *Cyclotella caspia* was present near Breton Island on September 10 with cell concentrations of 4,300/ml recorded.

In November, 1956, the river was again very low and very clear. Phytoplankton was nowhere abundant and this was apparently the season when populations were least dense in the eastern delta. The most abundant species was *Asterionella formosa*.

Samples taken in February, 1957, were from the river, which was again at flood stage, and from the plume which was very pronounced. Results were similar to those obtained in February, 1956.

During the period from May 1 to May 7 the river was still at flood stage and was very turbid. However, seasonal high tides flowing inward forced the plume into a narrow band near shore. Water temperatures had risen sharply since the winter sampling, and there was a distinct border between water from the river and from the Gulf as evidenced by phytoplankton populations and by hydrographic factors. Data from traverses across the plume into the Gulf are given in Tables 4 and 5. In the river and in the plume most plankton were of the *Melosira-Cyclotella* complex, and 10 species were identified. In the Gulf there was extreme diversity and patchiness of phytoplankton with over 30 species found at some stations. Dominant genera were *Chaetoceros, Thalassionema, Asterionella,* and *Skeletonema*. Cell concentrations were high for marine species in comparison to

TABLE 3

Seasonal conditions in the eastern Mississippi Delta with regard to phytoplankton abundance and hydrographic factors

Season	Area	Primary phytoplankton	Total cells/ml	Cl. ‰	Water temp. °C	PO_4-P ug at/l	SiO_3-Si ug at/l	Suspended solids mg/l	Remarks
June 1955	1	*Melosira spp.* *Cyclotella spp.*	1000	0.06	22.5	1.70	.....	161.0	River at flood stage
	2	*Cyclotella sp.* *Skeletonema costatum* *Chaetoceros affinis*	1300	15.71	23.7	3.00	.....	.....	
	3	*Cyclotella spp.*	1300	16.01	25.8	2.40	.....	24.0	
	4	*Skeletonema costatum* *Chaetoceros affinis*	2800– 3500	12.35– 15.24	23.6	....	....	53.0	
October 1955	1	*Cyclotella spp.* *Melosira spp.*	100	1.61– 2.41	28.0– 28.6	....	64.0– 68.0	12.0– 14.0	River clear, low
	2	*Scenedesmus spp.* *Cyclotella spp.* *Melosira spp.* *Skeletonema costatum*	500	6.03– 7.06	28.9	....	47.0– 61.0	34.0	
	3	*Thalassionema nitzschioides* *Nitzschia closterium* *Thalassiothrix fraunenfeldii*	400– 2000	15.83– 17.14	28.4– 28.8	....	9.6– 13.0	34.0– 38.0	
	4	*Thalassionema nitzschioides*	274– 2300	13.25– 14.33	27.0– 27.4	....	28.0– 36.0	30.0– 40.0	
	5	*Cyclotella sp.* *Gyrosigma sp.*	2300 5300	3.56– 4.10	....	....	40.0– 79.0	....	
February 1956	1	*Melosira granulata* *Coscinodiscus spp.*	3400	.04±.01	8.5±.5	.....	75.5	.....	River very muddy, swift
	2	*Melosira spp.* *Cyclotella spp.* *Skeletonema costatum*	1200	1.71	16.5	2.40	64.2	.....	

TABLE 3—Continued

Seasonal conditions in the eastern Mississippi Delta with regard to phytoplankton abundance and hydrographic factors

Season	Area	Primary phytoplankton	Total cells/ml	Cl. ‰	Water temp. °C	PO_4-P ug at/l	SiO_3-Si ug at/l	Suspended solids mg/l	Remarks
	4	*Skeletonema costatum* *Coscinodiscus spp.* *Rhizosolenis stolterforthii* *Chaetoceros spp.* *Asterionella japonica* *Nitzschia spp.*	20,000	15.91	15.9	.....	.....	.....	
	5	*Melosira spp.* *Cyclotella sp.*	2500	0.04	13.0	.....	.....	.....	
September 1956	1	*Cyclotella comta* *Melosira spp.*	1000	3.50	27.1	3.76	.....	.....	Clear, low river discharge
	2	*Melosira distans* *Coscinodiscus spp.*	100–270	6.01–13.50	27.5–28.1	3.56–4.09	.....	.....	
	4	*Cyclotella caspia* *Coscinodiscus spp.* *Thalassionema nitzschioides*	838–4300	15.1–18.4	25.8–26.0	2.81–2.91	.....	.....	
November 1956	1	*Asterionella formosa*	53	3.31	24.0	0.96	25.5	.....	Low river, clear water. Secchi reading 72 inches
	2	*A. formosa*	0–113	13.26	22.0	1.00	18.4	20.0	Secchi= 48–244 inches
	3	*A. japonica* *Melosira sulcata*	.....	19.71	23.6	.....	.....	58.4	
	4	.....	1	15.5	18.0	.....	.....	.....	

TABLE 3—Continued

Seasonal conditions in the eastern Mississippi Delta with regard to phytoplankton abundance and hydrographic factors

Season	Area	Primary phytoplankton	Total cells/ml	Cl. ‰	Water temp. °C	PO_4-P ug at/l	SiO_3-Si ug at/l	Suspended solids mg/l	Remarks
February 1957	1	*Melosira spp.* *M. granulata* *M. distans* *Cyclotella spp.* *C. comta* *C. meneghiniana*	2500 average	0.0– 0.04	10.0– 14.0	0.73– 1.77	60.0– 100.0	500.0– 600.0	River turbid, swift and flooded. Secchi disc= 3–6 inches
	2	*Cyclotella sp.* *Melosira spp.* *Plagiogramma vanheurkii* *Thalassionema nitzschioides*	574– 4500	0.07– 14.0	13.2– 16.0	.....	.....	.....	Secchi disc= 6–24 inches
	5	*Melosira sp.* *Cyclotella sp.*	6000	0.04	13.4	....	....	500– 600	
May 1957	1	*Melosira sp.* *Cyclotella sp.*	2700	0.07	19.5	0.36	.....	.....	River high and turbid. Secchi disc=1 inch
	2	*Cyclotella meneghiniana* *Melosira distans* *Asterionella japonica* *Chaetoceros spp.*	.. 304–3800	0.58– 6.54	19.4– 22.5	....	....	31.0– 168.0	Secchi disc= 36–144 inches
	3	*Chaetoceros sp.* *C. vanheurkii* *C. affinis* *Thalassionema nitzschioides* *Asterionella japonica* *Nitzschia sp.* *Skeletonema costatum* *Eunotia spp.*	233–1000	8.64– 17.93	22.3 23.9	....	....	16.0– 23.0	Secchi disc= 36–144 inches

TABLE 4

Diatom cell concentration and hydrographic conditions on a traverse from the plume to the Gulf in May, 1957

Station	Chlorinity ‰	Water temperature °C	Secchi disc m	Suspended solids mg/l	Concentration of cells number/ml	No. of species
985	08.64	22.2	1	23	605	19
986	14.08	24.5	2.5	14	441	10
987	15.11	23.9	4	20	866	20

TABLE 5

Closely spaced stations on a traverse in the Gulf in May, 1957

Station	Chlorinity ‰	Water temperature °C	Secchi disc m	Suspended solids mg/l	Concentration of cells number/ml	No. of species
990	13.69	23.0	1.5	21	463	20
992	15.69	22.7	2.0	19	662	26
993	16.29	22.7	2.2	23	998	26
994	17.20	22.7	2.5	16	233	26
995	17.7	22.2	3.5	....	411	19
996	17.90	22.7	3.7	20.0	752	46
996B, subsurface	17.93	22.7	....	20.0	312	29

those at other seasons, but concentrations were still less than those in the river and plume.

GENERAL REMARKS ON THE TEMPORAL AND HORIZONTAL DISTRIBUTION OF DELTA PHYTOPLANKTON

In order to summarize these data, a table has been prepared showing the horizontal distribution of the primary phytoplankton genera during each field trip (Table 6). A genus is listed as major if it formed more than 50 per cent of the population from any one sample in each area. The genus is also listed as major if it comprised more than 5 per cent of the population in the majority of stations in each area.

From Table 6, it is apparent that the river (Area 1) is the most uniform area throughout the year, with *Melosira* and *Cyclotella* the major genera at most times. At flood stage, the river always had a high cell concentration. These cells may have been transported many miles, since the cell concentration during February, 1957, was nearly homogenous throughout the river and the cells, although in poor condition, were still living. Phytoplankton concentrations were lowest in the fall when the stream flow was at a minimum.

These facts appear to be contrary to some of those reported by Kofoid (1903), Cilleuls (1926), and Pearsall (1923), as summarized by Blum (1956). These investigators reported a sharp decline in phytoplankton during periods of higher water. The decline was followed by an immediate "pulse" or "bloom." Kofoid, however, felt that stable water conditions might enhance phytoplankton production. In terms of the usual hydrographic measurements (chlorinity, water temperature, turbidity and current flow), the Mississippi is certainly most stable during times of high water. Transeau

TABLE 6

Horizontal distribution of primary phytoplankton genera in the eastern Mississippi Delta.
Cell number per milliliter given in parentheses

	Area 1 River	Area 2 Plume	Area 3 Gulf	Area 4 Breton Sound	Area 5 Blind Bay
June, 1955	*Melosira* (1109)	*Skeletonema* (2575)	*Cyclotella* (695)	*Skeletonema* (3022)	.....
	Clyclotella	*Cyclotella*	.....	*Chaetoceros*	.....
		Chaetoceros			
October, 1955	*Melosira*	*Melosira* (540)	*Cyclotella* (1293)	*Thalassionema* (1510)	*Cyclotella* (4306)
	Clyclotella	*Cyclotella*	*Thalassionema*	*Nitzschia*	.....
	.....	*Coscinodiscus*	*Thalassiothrix*	*Chilomonas*	.....
	.....	*Skeletonema*	*Nitzschia*	.....	.....
	.....	*Scenedesmus*	*Chaetoceros*	.....	.....
February, 1956	*Melosira* (3341)	*Melosira* (1216)	.....	*Skeletonema* (22097)	*Melosira* (2461)
	Coscinodiscus	.....	.....	*Chaetoceros*	*Cyclotella*
	.....	.....	.....	*Asterionella*	.....
September, 1956	*Cyclotella* (1031)	*Melosira* (244)	.....	*Thalassionema* (2536)	*Melosira* (291)
	.....	*Synedra*	.....	*Coscinodiscus*	*Cyclotella*
	.....	*Achnanthes*	.....	*Achnanthes*	.....
	.....	.....	.....	*Cyclotella*	.....
November, 1956	*Asterionella* (53)	*Melosira* (40)	*Melosira* (58)	*Chaetoceros* (1)	.....
	.....	*Asterionella*	*Cyclotella*	.....	.....
	.....	*Skeletonema*	*Thalassionema*	.....	.....
	.....	*Chaetoceros*	.....	.....	.....
	.....	*Navicula*	.....	.....	.....
February, 1957	*Melosira* (2665)	*Melosira* (2202)	.....	.....	*Melosira* (5171)
	Clyclotella	*Nitzschia*	.....	.....	*Cyclotella*
	.....	*Asterionella*	.....	.....	.....
	.....	*Thalassionema*	.....	.....	.....
May, 1957	*Melosira* (2667)	*Melosira* (653)	*Chaetoceros* (757)	.....	.....
	Clyclotella	*Asterionella*	*Skeletonema*	.....	.....
	.....	*Chaetoceros*	*Asterionella*	.....	.....
	.....	*Cyclotella*	*Eunotia*	.....	.....
	.....	.....	*Cyclotella*	.....	.....

(1916) stated that algae in fresh waters seemed to be most numerous at time of high water. This was true of diatoms in the Mississippi.

Melosira was absent from river samples taken in November, 1956. *Cyclotella* was still present, but the primary genus was *Asterionella*. Both fresh water and marine species of the latter genus were found. The disappearance of *Melosira* and the prominence of *Asterionella* was probably due to an increase in chlorinity from approximately 0.05 ‰ during high water to 3.07 ‰ during November, 1956. It is possible that this salt intrusion limited phytoplankton growth. The probable limiting factor during flood stage was turbidity of the water.

In Blind Bay (Area 5), the primary phytoplankton genera were the same as those in the nearby river. During flood stage a strong current of river water flowed into this bay. This area was not sampled in late spring or summer. At that time strong flushing action of spring tides could have introduced marine species into this bay and also increased the water temperature greatly.

In contrast to the relatively simple populations in the river and in Blind Bay, the populations in the plume (Area 2) were more complex. There was an increase in the number of major genera (see Table 6) due to an admixture of marine genera. From station to station within the plume, various dominant genera made up highly differing proportions of the total population. There were also great differences in the total cell concentration from station to station. At any one location in the plume cell concentration changed greatly from day to day.

There were two instances where the conditions in the plume paralleled those in the river. In November, 1956, the cell count was much lower than during other seasons. This low concentration was found in the river and generally throughout the Delta waters. Another instance of parallel behavior occurred in February, 1956, when a widespread plume of fresh, cold, muddy river water extended in a thin layer over the Gulf water. Such a plume has been traced far out to sea by Scruton and Moore (1953). This water was populated chiefly by *Melosira* which was also the major genus in the river.

The Gulf seaward of the plume (Area 3) was not sampled often enough to give a complete annual picture of the distribution of the phytoplankton. Bad weather hampered operations during the two winter field trips, and with the exception of the May, 1957, trip, only a few stations were occupied. The populations in this area were complex in the same manner as in the plume, with more major genera than in the river due to mixture of marine and fresh water genera, rapid changes in the population at any one location, and great differences from station to station. This complexity is illustrated by the description of conditions prevailing during the May, 1957, field trip, when the offshore area was sampled extensively. The total cell concentration varied from 16 to 3,781 cells/ml at 19 stations sampled. Among these stations, the ranges in per cent of total sample, for major genera were as follows: *Chaetoceros*, 0–61%; *Skeletonema*, 0–23%; *Asterionella*, 0–47%; *Thalassionema*, 0–45%; *Eunotia*, 0–58%; *Thalassiothrix*, 0–35%; *Melosira*, 0–28%; *Cyclotella*, 0–86%; and *Nitzschia*, 0–34%. Thus, at any one station a major genus was sometimes absent, but was dominant at another station within the offshore area.

It is apparent from Table 6 that the minimum total population in Area 3 was found in November, 1956, and in this respect this offshore area paralleled the other areas.

Breton Sound (Area 4) occupies an intermediate position between the river and the

offshore areas in terms of the complexity of its hydrography and phytoplankton populations. Because of its sheltered position away from the main mouths of the river and behind Breton Island, it is probably less affected by currents and tides than the rest of the areas. This is indicated by current maps published by Scruton (1956) and by the fact that even during flood stages, the plume does not extend into Breton Sound. The population in Breton Sound fluctuates from nearly none to a strong "bloom." A succession of major genera occurs in the Sound. *Skeletonema* was prominent from February to June, and was succeeded by a mixture of other genera later in the year, particularly by *Thalassionema* and *Chaetoceros*.

Counts of phytoplankton showed that during any one season, the concentrations did not differ from area to area. In the fall months, the concentration in the river was significantly less than at times of high river discharge (February or May). This was also true for the plume. In the Gulf, however, no significant seasonal differences were found.

Certain primary phytoplankton species were significantly associated with each other. Fager's (1957) method of testing for significant ($p = 0.05$) associations was used (Table 7). Two such associations were recognized by this test. One, the river population, consisted of *Cyclotella comta, C. meneghiniana, Melosira distans, M. granulata, Navicula gracilis,* and *N. rhyncocephala.* The other association, the Gulf population, con-

TABLE 7

Association of primary phytoplankton species with each other
— = no significant association, + = significant association @ .05 confidence level

Species	*Cyclotella comta*	*C. meneghiniana*	*Melosira distans*	*M. granulata*	*Navicula gracilis*	*N. rhyncocephala*	*Nitzschia seriata*	*Thalassionema nitzschioides*	*Skeletonema costatum*	*Asterionella japonica*	*Chaetoceros affinis*	*C. decipiens*	*C. diversus*	*Thalassiothrix frauenfeldii*
Cyclotella comta	0	+	+	—	—	—	—	—	—	—	—	—	—	—
C. meneghiniana	+	0	+	+	—	—	—	—	—	—	—	—	—	—
Melosira distans	+	+	0	+	+	—	—	—	—	—	—	—	—	—
M. granulata	—	+	+	0	—	—	—	—	—	—	—	—	—	—
Navicula gracilis	—	—	+	—	0	+	—	—	—	—	—	—	—	—
N. rhyncocephala	—	—	—	—	+	0	—	—	—	—	—	—	—	—
Nitzschia seriata	—	—	—	—	—	—	0	+	+	+	+	—	—	—
Thalassionema nitzschioides	—	—	—	—	—	—	+	0	+	+	+	—	+	+
Skeletonema costatum	—	—	—	—	—	—	+	+	0	+	+	—	—	—
Asterionella japonica	—	—	—	—	—	—	+	+	+	0	+	+	—	+
Chaetoceros affinis	—	—	—	—	—	—	+	+	+	+	0	+	—	+
C. decipiens	—	—	—	—	—	—	—	+	—	+	+	0	—	—
C. diversus	—	—	—	—	—	—	—	+	—	+	—	+	0	—
Thalassiothrix frauenfeldii	—	—	—	—	—	—	—	+	—	+	+	—	—	0

sisted of *Nitzschia seriata, Thalassiothrix frauenfeldii, Thalassionema nitzschioides, Skeletonema costatum, Asterionella japonica, Chaetoceros affinis, C. decipiens,* and *C. diversus.* Several other species were not significantly associated with any other. The members of one association were not associated with members of the other association.

The river association was found in the river and plume, and only rarely in the Gulf. Conversely, the Gulf association was found in the Gulf and plume, and only occasionally

in the river. The plume was thus an area where both associations were found. Blind Bay generally contained the river association, while Breton Sound generally contained the Gulf association. The river association was found in waters of 0–10 ‰ chlorinity, but generally not in more saline water; the reverse was the case with the Gulf association.

In our previous paper (Thomas and Simmons, 1960) we noted that at a plume station, occupied on three successive days, phytoplankton production increased seven-fold the second day and then decreased on the third day to approximately the original level. The phytoplankton concentration also decreased on this third day and this was accompanied by an increase in chlorinity. On the second day the major phytoplankton species at this station was *Melosira distans*, while more typically marine species were found as well on the third day. It is possible that this decrease in production was the result of the change in chlorinity which may have damaged cells of the freshwater species, *Melosira*. The fact that the river association is carried into the sea and is found at plume stations, but only rarely at Gulf stations, suggests that these freshwater species are destroyed by the increased chlorinity. The fate of these species is worthy of further investigation. Sediments taken just off the mouth of Pass-a-Loutre were examined and contained many cells of these freshwater species.

Comparison With Other Areas

King (1949) examined samples taken off the west coast of Florida and found that conditions there were similar in many respects to those in the Mississippi Delta. The actual volume of plankton was very low compared to northern waters but the variety was much greater. The Delta, in spring, is apparently even more diverse, since over 30 genera of diatoms were obtained from a 60 ml unconcentrated sample as compared to 11 genera obtained from 1600 liters of water in Florida. Packed cell volumes of unconcentrated water samples were obtained in the Florida waters. One nearshore sample there contained 0.0806 ml of solids per liter of water. This was exceptionally high for that area, the next highest value listed being 0.0359 ml. Samples collected near the 10 fathom line gave values ranging from 0.0012–0.0271 ml per liter of water. The figure given for May from this location was 0.0043. As a comparison, the calculated value at the 10 fathom line for May, in the Delta, was about 0.0050 ml. All of these figures include sediment and the Florida figures include zooplankton as well. May, of course, was the month when phytoplankton appeared to be most abundant in the Delta along this depth line, whereas August was more productive in Florida water. However, from an examination of all of the values given for Florida stations in King's survey it would appear that the two areas are quite similar, *i.e.*, there is a peak in May or June with another peak occurring in late summer or fall, and a decline later in the year. The actual number of phytoplankton cells in Florida is somewhat less than in Delta waters, a a difference possibly explainable in that a Clark-Bumpus net was used in Florida while unconcentrated water samples were used in the Delta.

Curl (1959) listed 90 species of diatoms from the northeastern Gulf of Mexico, primarily from Apalachee Bay and Alligator Harbor. In many ways the phytoplankton of that area resembled that of the eastern Mississippi Delta. Notably absent from Florida waters was the genus *Cyclotella* and several species of *Melosira*. Species common in the Delta and absent or uncommon in the northeastern Gulf include *Coscinodiscus nitidus, Chaetoceros compressus, C. costatus, C. pelagicus, C. brevis, Diatoma spp., Eunotia spp.,*

Plagiogramma vanheurkii, Achnanthes spp. and *Navicula spp.* Forms found to be abundant in the northeastern Gulf but absent or rare in the Delta include *Eupodiscus radiatus, Certatulina pelagica, Triceratium favus, Eucampia cornuta, Rhizosolenia alata,* and *R. stolterforthi. Biddulphia aurita, Chaetoceros gracile, Achnanthes spp.*, and *Cocconeis spp.*, listed by Curl as rare in the Gulf or not previously reported, were fairly common in the eastern Mississippi Delta. *Chaetoceros dichaeta* given by Curl as a first record from the Gulf was not found in the Delta. Many forms were probably found in the Delta but not in Florida because of the proximity of a large river. There were extreme patchiness and irregular distribution of species in both areas but in the Delta most phytoplankton was found near the surface whereas in the Florida waters there were no significant differences between depth samples.

Freese (1952) found more than 70 species of diatoms in the area of Rockport, Texas, although the blooms reported in his paper occurred several months before the general peak in the Delta. However, the heavy bloom reported in February near Breton Island corresponds well to some found in equally protected Texas bay areas. In Texas some oceanic species such as *Thalassiothrix frauenfeldii* and *Rhizosolenia alata* appeared first in the spring at Gulf stations and the progressed further inshore (Freese, 1952). This might indicate that, in the Delta, the May peak is caused by a similar inward progression of diatoms in May or June. Many forms, of major importance in Texas bays, were not abundant off the Mississippi Delta. The presence of several cold water species in Texas waters, notably *Skeletonema costatum,* was attributed to heavy runoff from the Guadalupe River and this form was also very abundant in the Delta near the water source. However, this species was found by Simmons to be abundant in September, 1956, in the Texas Laguna Madre, a hypersaline bay.

Simmons (1959) also found that tychopelagic diatoms were abundant in the hypersaline Laguna Madre and that blooms occurred in September after tidal flats were flooded by high tides. Many species found in the Gulf areas of the eastern Delta were also present in the Laguna Madre but the major phytoplankton in the latter case were blue-green algae.

Bigelow (1926) found an entirely different seasonal trend in the Gulf of Maine with the lowest numbers occurring in late February and early March and the highest peak, as a rule, in April. The composition of the plankton varied greatly from that of the Mississippi, and the counts were much higher.

In some respects the diatom flora in the Delta resembled that found off southern California. Allen (1936) found that such forms as *Chaetoceros sp.* were most abundant in the spring and that filiform genera, such as *Thalassionema sp.* were more abundant in the fall . Perhaps the chief difference between the areas is the larger number of littoral and tychopelagic forms found in and near the river and swamps.

Smayda (1957) found that most of 75 species recorded in lower Narragansett Bay were diatoms, but in some instances dinoflagellates were present in greater concentrations. The peaks found there for *Skeletonema costatum* and *Asterionella japonica* were reversed seasonally from those found in the eastern Mississippi Delta.

Conover (1956) reported that in Long Island Sound diatoms were prominent except during the summer when these were largely replaced by dinoflagellates and flagellates. She reported a clear-cut succession of species and changes in abundance from year to

year. A variation in abundance was noted in the eastern delta, but there was no clear-cut succession except in isolated areas.

Summary

1. Phytoplankton collections were made from 134 stations in the eastern Mississippi Delta region. The entire region was divided into five general areas representing different habitats. Seasonal variations in phytoplankton composition and quantity were analyzed, and an attempt was made to correlate these variations with various ecological factors. A partially annotated checklist was prepared with notes in the phytoplankton species found during the survey.

2. Over 200 species of phytoplankton, most of which were diatoms, were noted during this survey. Two associations of phytoplankton species were recognized. One, the river association, consisted of species of *Cyclotella*, *Melosira*, and *Navicula*. The other, the Gulf association, was made up of species of *Nitzschia*, *Thalassionema*, *Thalassiothrix*, *Skeletonema*, *Asterionella*, and *Chaetoceros*. Both associations were found in a zone of mixing of fresh water with sea water, designated the primary plume.

3. During the February trips, river discharge was very great and the plume extended far out into the Gulf. The river population was found at all plume and river stations and in Blind Bay. However, samples taken in more saline water underlying the plume and in Breton Sound contained a typical marine population. Cell numbers were relatively higher than in the fall months.

4. In May and June, conditions were similar to those of February. However, water temperatures were higher and the plume did not extend as far to sea, being modified by incoming high tides of the spring of the year.

5. In September, some marine forms were present in the river along with the usual river population. Chlorinities were also greater at the river station. The plume station showed variable populations and chlorinities. Cell concentrations continued to be relatively greater than those of the fall months.

6. Samples taken during October and November contained less phytoplankton than those taken at any other season. Although chlorinities approached 3.0‰ in the river, the usual river population was found. The river was low and much clearer than at other seasons. A mixed river and Gulf population was found at plume stations, and a Gulf population was present at Breton Sound and in the Gulf.

7. In comparison with other parts of the seas, the eastern Mississippi Delta has a low concentration of phytoplankton, but in comparison with other nearshore areas in the Gulf of Mexico, both the cell concentration and the number of species are large.

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Fishes of the Río Tamesí and Related Coastal Lagoons in East-Central Mexico[1]

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Abstract

A total of 11,043 specimens of fishes was obtained in 66 collections from the tributaries of the Río Tamesí and from a coastal lagoon near Tampico. Sixty species of fishes are now recognized from the area, 23 of which are fresh-water forms and 37 of which are considered to be euryhaline. For each species information is given, if available, regarding the following: nomenclature, distribution, salinity relations, general ecology, food habits, and reproduction.

The 23 fresh-water species include strictly fresh-water forms (15), sporadic invaders of low salinity water (4), and frequent invaders of low salinity water (4). The 37 euryhaline species include anadromous forms (4), catadromous forms (2), frequent invaders of fresh-water (5), sporadic invaders of fresh-water (9), and marine species which are facultative invaders of low salinity water (17). Twelve of the species are considered to be endemic in the Pánuco-Tamesí system, all of which are strictly fresh-water forms.

For both the fresh-water fishes and the littoral marine fishes, eastern Mexico represents a zone of transition between the temperate and tropical faunas. Among the fresh-water species of the Tamesí, representatives of southern families slightly outnumber representatives of northern families (13:10). Among the euryhaline species, representatives of southern families greatly predominate over those of northern families (35:2). Analysis of habitat distribution of the fresh-water fishes of the Tamesí reveals that those of southern derivation inhabit primarily the small upstream waters, whereas those of northern affinity are chiefly inhabitants of larger and downstream waters. These phenomena are discussed in terms of faunal centers and barriers to dispersal.

[1] Contribution No. 6 from the Laboratory of Hydrobiology, Department of Biology, Marquette University.

Introduction

In 1950 the writer initiated a series of studies on the ecology of aquatic communities in the headwaters of the Río Tamesí drainage in east-central Mexico. A portion of this material was incorporated into his doctoral dissertation presented to the faculty of the University of Minnesota (Darnell, 1953). Although the studies were primarily concerned with the composition and trophic structure of the subtropical aquatic communities, problems of taxonomy in the various aquatic groups inhabiting this poorly known area have delayed the appearance of the general ecological treatise. This delay has been occasioned, in part also, by the hope that the manuscript of Hubbs and Gordon on the fishes of northeastern Mexico, imminent for over twenty years, would finally make its appearance. With the recent death of Dr. Gordon the present writer is hesitant to delay further the publication of his ecological work and so has prepared this paper as a background for the ecological study already accomplished, but still unpublished.

It was originally intended that the present article should include only the strictly fresh-water fishes of the Tamesí system. This was rendered impossible by the following circumstances, the lack of detailed habitat data for most of the species in the important coastal collections of Jordan and Dickerson (1908), the fact that the writer's Laguna de Chairel collections contained a number of typically brackish water or marine species, and also by the fact that many of the headwater species probably or definitely do not honor the bounds of strictly fresh water. Thus, in the absence of any sharp dividing line, it was decided to include the work of Jordan and Dickerson (1908) and to summarize the present status of our incomplete knowledge of these forms as a point of departure for future work.

Several species, so far not recorded from the drainage, are expected to be found when the larger streams and the lagoons around Tampico are adequately sampled. None are included in the present work, however, unless specimens have been reported directly from the drainage (or from coastal areas near the drainage in the case of *Fundulus similis* and certain forms included in Jordan and Dickerson's collections). This excludes a number of fresh-water, brackish-water, and marine species whose known distributional ranges extend on both sides of the Tamesí, as well as certain species previously encountered in the Río Pánuco but for which specimens have not yet been taken from the Río Tamesí.

Bailey, Winn and Smith (1954) and Bailey (1956) have recently discussed the basic concept of subspecies in fishes with considerable clarity and reason, and they have cast doubt, not only upon the validity of a number of existing subspecies designations (some of the doubtfully subspecific forms being found in the Tamesí), but also upon the concepts on which many of the old subspecies were erected. For reasons best expressed by these authors no subspecies designations are given in the present paper. Future work is required to determine the nature and extent of variation in the local populations, their divergence from other such populations, the clinal nature of such divergence, and the extent to which this may be due to environmental factors. Invalid manuscript designations which have escaped into the literature with unfortunate frequency are, of course, not employed here.

A number of the fish species listed herein were first described in the monumental work of Cuvier and Valenciennes (1828–49). As noted by Bailey (1951) the authorship

of all such species can and should be determined. In the present work only the appropriate single author is given for each of these species.

Materials and Methods

Material for the present study was collected during three trips to Mexico in the period 1950–53. The first trip was accomplished April 1–June 7, 1950, the second March 13–June 16, 1951, and the third December 20, 1952–January 3, 1953. Thus, a total of six months was spent in Mexico during the spring, early summer, and winter seasons. Most of the fish collections were made with a 20 or 40 foot (¼ inch mesh) minnow seine with native help and represent shallow upstream habitats. On the last trip a 150 foot (¾ inch mesh) bag seine was taken and successfully employed in some of the larger waters. Additional specimens were taken by fyke net, hook, spear, minnow trap, gill net, and plastic window screening. Considerable time was spent observing the habitat distribution and behavior of fishes, especially in the crystal clear waters of the upper stretches of the Río Sabinas. Such observation was particularly important in relation to groups which normally inhabit the deeper waters and such wary species as the cichlids which make frequent use of shallow areas but which are difficult to capture by seine.

Most of the preliminary identifications were carried out by the writer. Robert R. Miller of The University of Michigan Museum of Zoology and the late Myron Gordon of the American Museum of Natural History checked the preliminary identifications on a number of the fishes, but final species determination on almost all specimens was accomplished by Carl L. Hubbs. Food analyses were carried out essentially in accordance with the procedure previously outlined by the writer (Darnell, 1958). In order to provide a generalized picture of the true food relations of each species, specimens for food analysis were picked from several size classes of both sexes taken at different localities in day and night collections. Where this was not possible it was approximated.

Collection and Disposition of Specimens

During the field work a total of 11,043 specimens of fishes were taken from the Río Tamesí drainage in seines, fyke nets, and minnow traps. About a dozen additional specimens were procured by other means. In all, 66 collections were made in the various portions of the drainage as follows: Río Sabinas and tributaries 54 (reduced to 31) collections (6,768 specimens), Río Frío and its tributary, the Río Boquilla, six collections (2,538 specimens), Río Mante and its tributaries, four collections (1,272 specimens), Río Guayalejo, a single collection (221 specimens), and the Laguna de Chairel at Tampico, a single collection (244 specimens). By far the greatest attention was paid to the fishes of the Río Sabinas where the general ecological study was in progress, and in order to reduce the number of stations for presentation here the data for many adjacent collections were lumped. Due to lack of time, gear, and transportation facilities the fishes of the larger streams as well as the coastal lagoons around Tampico were very inadequately sampled. In addition to the collections mentioned above, the writer has examined most of the material taken by Meek in 1903 from the Río Guayalejo, but specimens reported from the Tampico area by Jordan and other early workers have not been seen.

Most of the 1950–51 material has been deposited in the Chicago Natural History Mu-

seum. Poorly preserved specimens of the common species were discarded. For the remaining collections, specimens of a given species taken from the same stream during the same year have been lumped and have received a single (CNHM) catalog number. Representative specimens from the 1950–51 material are also being deposited in the fish collections of the Zoology Department of the University of Minnesota, the Instituto de Biología, Mexico City, and the writer's private collection. The 1952–53 material has been deposited in its entirety in the Tulane University (TU) collections. For the most part each field collection was kept distinct at Tulane, but in several cases nearly identical collections made the same day were lumped.

History

The history of ichthyofaunal investigation of the Río Tamesí area may be divided into two overlapping, but basically distinct, periods, the period of description and the period of synthesis. The first, from 1901 to 1908, was marked by the appearance of three major taxonomic works (Jordan and Snyder, 1901; Meek, 1904; and Jordan and Dickerson, 1908). The second, although foreshadowed by two papers of Regan (1905, 1913), really began in 1926 with Hubbs' study of some of the poeciliid fishes of the drainage system, and it has continued on an intermittent basis until the present time. This second period is characterized by the systematic analysis of species and genera which may extend into the area, especially from the north, but, for the most part, such studies have dealt only incidentally with the fishes of this drainage. It may fairly be stated that, after a flurry of early attention, the ichthyofauna of the Río Tamesí has lain, nearly forgotten in the literature, for half a century.

The first reference to the fishes of the Tamesí area appears to have been that of Duméril (1870), who reported the alligator gar from Tampico. Jordan and Snyder (1901) published on fish collections from headwaters of the Río Pánuco (Río Verde near Rascón), listing several species which have subsequently been reported from the Río Tamesí. They also included several species from the vicinity of Tampico including gars and catfishes obtained in the local fish market. Shortly thereafter, S. E. Meek (1904) published an extensive monograph on the fresh-water fishes of Mexico north of the Isthmus of Tehuantepec, which included the first direct information on fishes of the headwaters of the Tamesí system. In a single collection from the Río Guayalejo at Forlón, Meek recognized 16 species including four which were described as new. Meek also provided further collections from the headwaters of the Río Pánuco (Rascón, Valles, Río Verde). Including those which had previously been reported from the Tampico area, Meek's collection brought the number of species recognized from the Tamesí to 21.

In 1908 Jordan and Dickerson published an important work on the "marine" species collected from Vera Cruz and from "the muddy estuary of the Río Pánuco and elsewhere along the sandy shores." Many of these specimens must have been taken from brackish water (see Station 9A). In this paper the authors listed 28 species from the Tampico area and included one without locality data which may have been taken from Tampico. Twenty-four had not previously been recorded from the area. Most of the "marine" species listed by these writers are known to be either frequent inhabitants or, at least, occasional visitors in water which is fresh or nearly fresh, and a number of them have

been taken in the present study from the headwaters of the Tamesí or from the nearly fresh Laguna de Chairel at Tampico.

The British ichthyologist, C. Tate Regan, in 1905 published the first of four papers relating to the fishes of the Pánuco-Tamesí system. In this initial work he attempted to clarify the cichlid fishes of the drainage, and he reduced to synonomy one of the species described by Jordan and Snyder (1901) and listed doubtfully by Meek (1904). In 1908 Regan described a new species of cichlid on the basis of two specimens which were said to have been taken from the vicinity of Tampico. In the same year he completed the ichthyological section of the monumental Biología Centrali-Americana (Regan, 1906–1908). Although this work was concerned chiefly with the Central American fauna, six of the Pánuco-Tamesí species were mentioned. In his last paper of importance in relation to the fishes of the area, Regan (1913) attempted to straighten out the taxonomy of certain of the poeciliid fishes, especially by means of the detailed characteristics of the remarkable gonopodium of the males. In this study Regan also extended the known range of the Amazon molly to the Tampico area on the basis of misidentified specimens.

The second period of ichthyological work relating to the fishes of the Tamesí area has been dominated by Carl L. Hubbs. In his publications on the fishes of eastern Mexico he has cleared up numerous taxonomic problems and has aided in relating the fauna of the Pánuco-Tamesí system to that of other areas. In 1926, having reexamined Meek's early collections from the Pánuco-Tamesí drainage, Hubbs described therefrom three new species of the genus *Gambusia*, two of which were present in the Forlón material, and the third of which has appeared in collections from the Tamesí by the present writer. In his paper on the catostomid fishes of eastern North America, Hubbs (1930) reduced Meek's nominal species of sucker to the synonomy of a wide-ranging species from the southern United States. In his 1936 paper on the fishes of the Yucatán peninsula Hubbs discussed several of the species which had been recorded from the Tamesí, and he pointed out that the ariid catfish obtained by Jordan and Dickerson (1908) from Tampico was, in reality, *G. felis*, a widespread estuarine species. In 1937 and 1940 Hubbs published on the fish fauna of streams north of the Tamesí area, discussing a number of the Tamesí species. In a series of papers (C. L. Hubbs, 1933, 1934, 1955; C. L. Hubbs and L. C. Hubbs, 1932, 1946) the same investigator, twice co-authoring with his wife, analyzed the unusual breeding behavior of the "double crossing" Amazon molly, a species which he noted to be present in the Tamesí, and in 1932 they mentioned receiving live specimens of this fish from Forlón, the site of Meek's early collection. Finally, in 1954 Hubbs reduced one of the minnows of the Tamesí drainage to the synonomy of a wide-ranging northern shiner.

The late Myron Gordon carried out numerous studies on the genetics and ecology of the poeciliid fishes of the Río Papaloapan in Vera Cruz, and a number of his papers refer to species which inhabit the Río Tamesí or to their close relatives (for bibliography see Gordon, 1947). Hubbs and Gordon (1943) and Gordon (1953) discussed the systematics and ecology of the xiphophorin fishes of the Río Pánuco, providing information on species which also inhabit the Tamesí.

In 1947 the Mexican ichthyologist, Fernando DeBuen, published a catalog of the Nearctic fishes found on Mexican soil, in which he outlined the zoogeographic provinces of Mexico, listing the drainages, and sketching the ichthyofauna of each. Announcing his intention of continuing the series with a detailed discussion of each faunistic region,

he proceeded to characterize the Nearctic fauna. Much of this discussion bears directly upon the fauna of the Pánuco-Tamesí system, but, unfortunately, with DeBuen's move to South America the series has apparently been abandoned.

Another Mexican ichthyologist, José Alvarez, after visiting various libraries, museums, and laboratories in the United States, published in 1949 a historical résumé of the ichthyological work accomplished in Mexico up to that time, and this was followed (1950a) by a taxonomic bibliography of the Mexican fresh-water ichthyofauna. Both of these papers have been important aids in the preparation of the present manuscript. Alvarez (1950b) also published a compilation of taxonomic keys to the fishes of the Mexican continental waters. Although this work brings together a great deal of scattered literature, it was critically reviewed by Miller (1951), who pointed out numerous errors and oversights. Other investigators whose works are of importance in the understanding of the taxonomy or distribution of species inhabiting the Río Tamesí or the coastal lagoons include the following: Baughman and Springer (1950), a shark; Darnell (1953, 1955, 1956), various headwater species; Ginsburg (1931, 1932, 1933), several gobies; Hildebrand (1955), a croaker and a sheepshead; Clark Hubbs and Brown (1956), a minnow; and Miller (1955, 1959), cyprinodontid fishes of the genus *Fundulus*, as well as an eleotrid. The excellent but unpublished thesis of Curran (1942) contributes to the understanding of the gerrids.

Geography and Geology

The Río Tamesí system is located in east-central Mexico a few kilometers south of the Tropic of Cancer in the northern sector of the Tampico Embayment. This embayment is an alluvial plain which slopes gently eastward from the Sierra Madre Oriental to the Gulf of Mexico. Its width varies from 100 to 150 kilometers, and its height at the foot of the mountains averages around 100 meters above sea level. Immediately west of the area rise the rugged front ranges of the Sierra Madre Oriental, and to the north lie a series of complex dipping anticlines and basalt mesas (see Fig. 1). The geology of the Tampico Embayment area has been discussed by Muir (1936) and Heim (1940).

At the present time the front ranges of the Sierra Madre Oriental consist of parallel north-south anticlinal ridges separated by shallow synclinal valleys. They rise abruptly from the coastal plain, and west of the embayment they reach an altitude of over 1300 meters. In the northern sector of the embayment the front range is broken by the valleys of the Ríos Guayalejo and Boquilla, both tributaries of the Río Tamesí.

Waters of the Río Tamesí enter the Gulf of Mexico near Tampico, which is located about midway between the Río Sota la Marina, on the north, and the Río Tuxpan, on the south. The Soto la Marina and the Tuxpan are about three hundred kilometers apart, and the intervening coastline is very regular. Between Tampico and the Soto la Marina lies a narrow sandy strip punctuated with coastal lagoons. South of Tampico the Laguna Tamiahua lies inside the coastal strip of sand dunes. This large lagoon extends about two-thirds of the way to the Río Tuxpan and is apparently connected with that river by a narrow southward extension. In the lowland immediately west of Tampico lies an extensive series of marshes and shallow lagoons.

Precipitation

Rainfall in the Tampico Embayment area is markedly seasonal and varies in relation

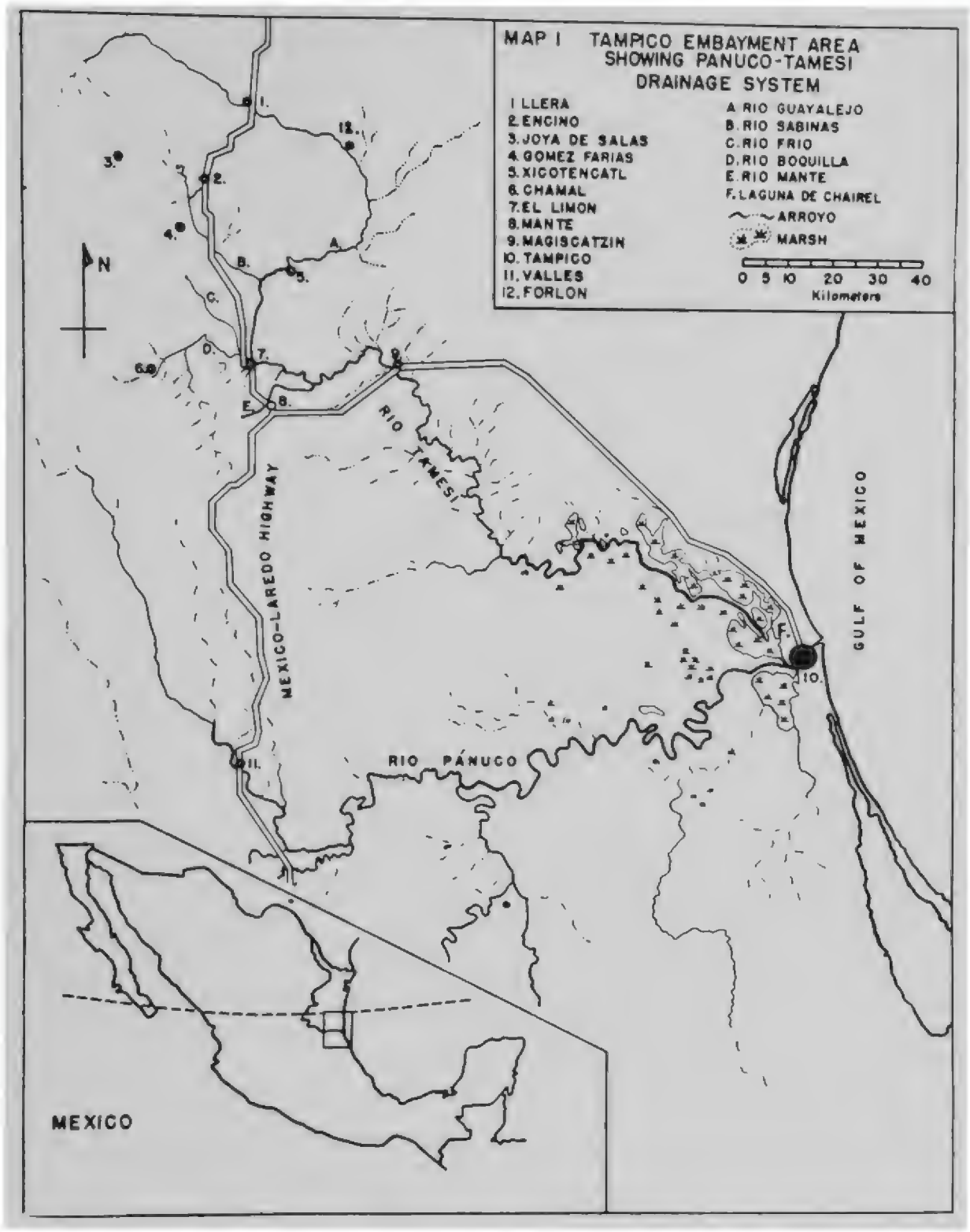

FIG. 1. Tampico Embayment area showing the Pánuco-Tamesí drainage system (Inset depicts the general location of the area below the Tropic of Cancer in southern Tamaulipas, Mexico.) Note the limited extent of the drainage during the dry season. Only the larger arroyos of the wet season drainage are shown. This figure is a composite based upon several maps of the area, and since all have been found to contain many errors in detail, the composite may reflect such inaccuracies except in areas of most intensive study.

to the local physiography. In late spring, summer, and early fall easterlies from the subtropical high belt bring moisture from the Gulf of Mexico. Passing inland these winds meet no major barrier until they reach the eastern front of the Sierra Madre. Here they rise, and, cooling, drop their moisture. Thus, although most of the embayment proper receives little direct rainfall, the precipitation increases sharply as the mountains are approached, and the average rainfall of the front ranges has been estimated to be about 2,000–2,500 mm annually (Darnell, 1953). The wettest months are June and September.

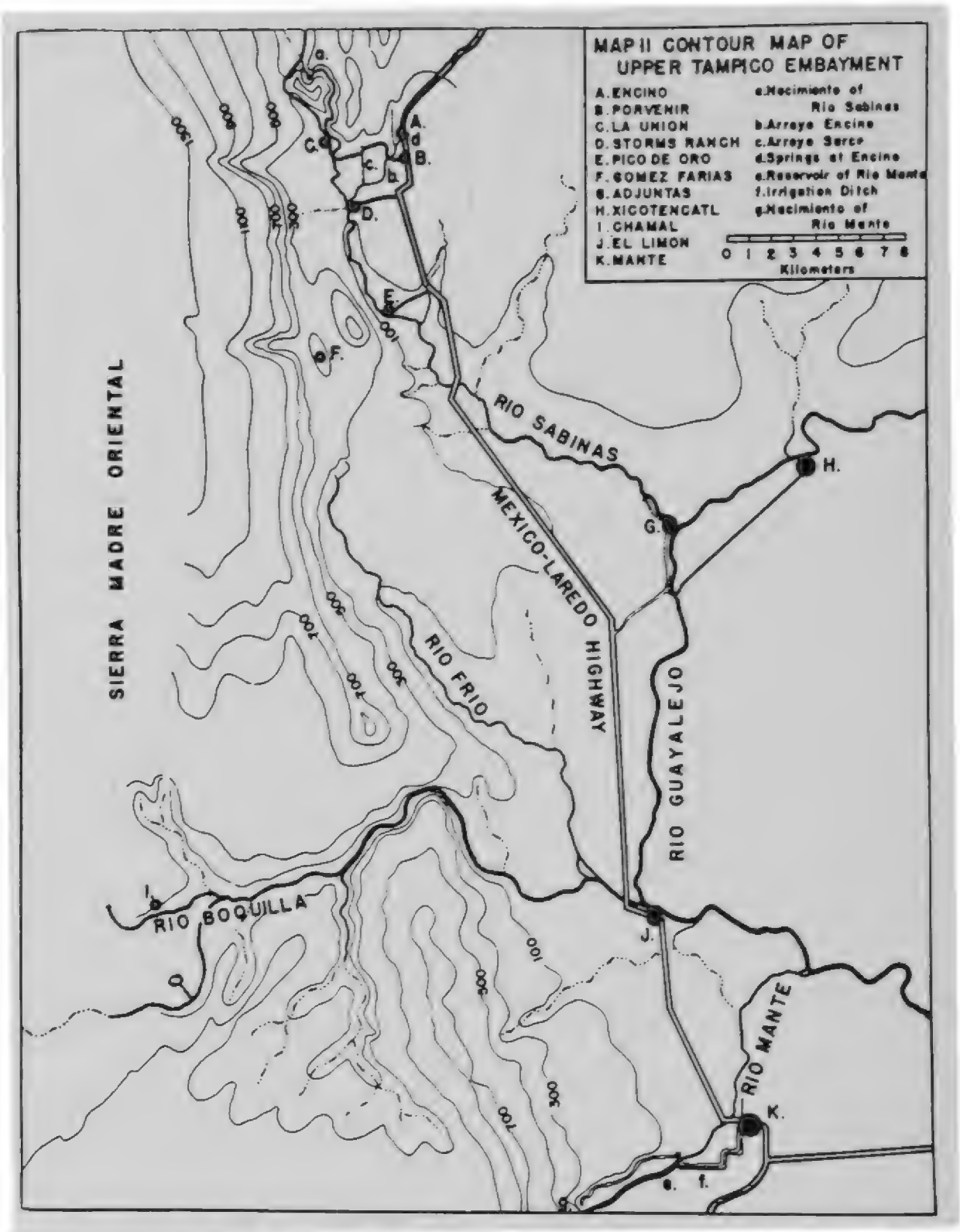

FIG. 2. Contour map of the upper Tampico Embayment area. Note relationship of headwater streams with the Sierra Madre. Details of the Río Sabinas and the Arroyo Encino should be accurate, but smaller features of the other streams should be accepted with caution. Contour intervals are given in meters.

Drainage

The Tampico Embayment is drained, in the south, by the Río Pánuco and, in the north, by the Río Tamesí which join shortly before entering the Gulf. Several tributaries of the Río Pánuco originate in the high central plateau of Mexico and traverse the Sierra Madre Oriental in spectacular cascades and waterfalls. Others arise as large springs or "nacimientos" (= birth) fed by underground rivers from which blind cave fish are known. Among the tributaries of the Río Tamesí, only the northernmost, the Guayalejo, begins high in the mountains. The remainder arise as small springs or large nacimientos in shallow valleys at the foot of the Sierra, and they lie almost entirely within the Tampico Embayment. Quite different in details of origin, the Ríos Guayalejo,

Sabinas, Frío, Boquilla, and Mante join, one by one, to form the Río Tamesí which meanders coastward (see Fig. 2).

Río Guayalejo

The northernmost tributary, the Río Guayalejo, is born high in the Sierra Madre in the synclinal valley of Juamave. After traversing the Sierra through a narrow canyon, the stream then bends southward into the northern edge of the Embayment. In its lowland portion the Guayalejo contains numerous deep pools and exhibits modest flow during the dry season, but the broad bed and steep banks attest to a greatly increased flow volume during the rainy season. As in the case of the other streams of the Tamesí drainage, the Río Guayalejo receives numerous arroyos which provide rapid surface drainage during times of heavy precipitation, but which during the dry season may exhibit reduced flow, isolated pools, or no water at all. Proceeding southward through the embayment the Guayalejo receives in turn the Ríos Sabinas, Frío, and Mante before heading coastward as the Río Tamesí.

Río Sabinas

The Río Sabinas, the second tributary, takes origin in a rocky canyon at the foot of the Sierra Madre about 13 kilometers north of Gomez Farías. The Nacimiento of the Sabinas is a limestone basin filled with water to a depth of 18 meters and has an estimated surface area of a little less than one acre. This basin is fed by an underground river, and during the dry season the Río Sabinas, as it leaves the Nacimiento, exhibits a flow volume estimated at several cubic meters per second. Below the Nacimiento for three or four kilometers the Río Sabinas traverses a narrow, winding, rocky canyon where the current is generally swift and where habitat conditions are highly variable. Leaving this canyon it continues southward paralleling the base of the Sierra, and here it is characterized by longer pool areas and less abrupt habitat transitions. About six kilometers below the Nacimiento, at Storms' Ranch, the Río Sabinas receives one of its major tributaries, the Arroyo Encino. Below the ranch the river continues southward to about the level of Gomez Farías where it abandons the mountains and swings eastward. Beyond this point riffles are less prominent, and the river continues as a sluggish stream past the Mexico-Laredo highway to its junction with the Río Guayalejo at Adjuntas. Below the highway bridge the Sabinas passes into a shale exposure. As seen at Adjuntas this shale produces a deep fine powder which, during the dry season, coats all the surrounding landscape, including the vegetation. In the Sabinas this material forms a deep powdery silt-like bottom and imparts to the warm sluggish water a tawny, turbid appearance. No fish collections were attempted here, although certain of the more tolerant species collected in the Río Guayalejo opposite the mouth of the Sabinas may also be present in the lower portion of the Sabinas itself. This lower stretch of the Río Sabinas undoubtedly serves as an effective barrier to the dispersal of headwater fishes, at least during the dry season.

Major tributaries of the Río Sabinas include the Arroyo La Flor and the Arroyo Encino. The former lies in the rocky canyon above the Nacimiento of the Sabinas, and during the rainy season its waters enter the Sabinas at the Nacimiento. Although this arroyo was not visited during the wettest season, ample evidence indicated that following heavy rains it contains a torrential stream which may achieve an average depth of two

or three meters. In the dry season its bed exhibits a chain of spring-fed ponds connected with each other and with the Nacimiento by a slight current. Some of the connections are subsurface, and all probably act as barriers to interpond dispersal of the fishes.

The Arroyo Encino begins as a series of small springs at the village of Encino on the Mexico-Laredo highway about eleven kilometers northeast of Gomez Farías. After meandering through the scrub forest for about five kilometers this arroyo joins the Río Sabinas at Storms' Ranch. Due to the presence of the springs, this arroyo contains pools connected throughout the dry season by small, flowing riffles. It receives one major tributary, the Arroyo Sarco, which during the dry season supports only a series of disconnected or slightly connected ponds.

Río Frío

The Río Frío begins at the foot of the Sierra a short distance south of Gomez Farías. Although not visited by the writer, the Nacimiento of the Río Frío is said to consist of a series of small springs whose combined flow during the dry season is considerably less than that of the Río Sabinas. Like the Sabinas, however, the Río Frío passes southward for several kilometers, and then swinging to the southeast it leaves the mountains to join the Río Guayalejo. Two or three kilometers above its junction with the Guayalejo and about twenty-five kilometers from its source the Frío receives its major tributary, the Río Boquilla. Below this junction the Frío is a large, turbid, sluggish lowland stream. As in the case of the lower sector of the Río Sabinas, the lower stretch of the Río Frío undoubtedly acts as a habitat barrier to the dispersal of upstream fishes.

The Río Boquilla drains the valley of Chamal several kilometers southwest of Gomez Farías. Although a few springs are found in the headwaters of the Boquilla, most of the arroyos as well as the upper portions of the Río Boquilla itself are devoid of current in the dry season. During the course of the present work a small shallow lake was encountered in the Chamal valley, and there is evidence that lake conditions were much more extensive in this valley in the past than at present. After leaving the Chamal Valley through a narrow breach in the low El Abra ridge, the Río Boquilla passes southeastward to its junction with the Río Frío.

Río Mante

The Río Mante flows as a large stream from a cave in the eastern face of the El Abra ridge about eight kilometers southwest of Ciudad Mante. Four or five kilometers from the source a dam has been placed across the river creating a reservoir which apparently extends all the way back to the Nacimiento. Diversion canals remove water from the reservoir just above the dam, and by means of open ditches they distribute this flowing water throughout the countryside primarily for irrigation purposes but also for human consumption. Immediately below the dam the bed of the Río Mante, deprived of most of its water supply, contains during the dry season a series of pools in the pavement limestone. A few hundred meters downstream, however, the Río Mante takes on the aspect of a small headwater stream and consists of small rocky pools with alternating riffles. Possessing little flow during the dry season the Río Mante soon becomes polluted, and in the immediate vicinity of Ciudad Mante the river is one long, heavily-polluted pool. Near the junction of the Río Mante with the Río Guayalejo, as shown on various

maps of the area, the adjacent land apparently becomes low and swamp-like. This swampy area has not been investigated in the present study.

Río Tamesí

After receiving the headwater tributaries the Río Tamesí meanders coastward, joined here and there by dry arroyos. Although it is bounded by high steep banks, it is a sluggish lowland stream during most of the year. Nearing the coast the river passes a series of marshes and lagoons which are rather extensive, even during the dry season. Sixteen kilometers inland, after traversing the Laguna de Chairel, the Tamesí joins the Río Pánuco, and they flow to the Gulf as a single river. This area has been well described by Jordan and Snyder (1901) as follows: "At Tampico the Pánuco, a very large river, receives the Río Tamesoe. With the two, a number of large, shallow lagoons are connected. Salt tide water backs up into the rivers and lagoons for some distance above the city. The lagoons are marshy in most places, the rushes and shrubs growing out into the water for a long distance. The bottom and shores are usually of a sticky blue clay, although there are sandy beaches in some localities." As pointed out previously, brackish-water coastal lagoons are also found along the Gulf coast for some distance both above and below the mouth of the Pánuco-Tamesí river system.

Collecting Stations in the Río Tamesí System

Río Sabinas

Series 1. Arroyo Encino series from springs at Encino, where the arroyo begins, to its junction with the Río Sabinas at Storms' Ranch (7 km northeast of Gomez Farías).

Station 1A. April 20, 1951. R. M. Darnell and natives (field no. E-1). Small upper spring above village of Encino (about 100 m east of the Mexico-Laredo highway). Water clear, current moderately slow; spring about 2 m across, ⅔ m deep; bottom of sand and shale; no vegetation; shaded. Fishes collected by seine, and estimated half of resident population taken. CNHM colls.

Station 1B. May 22, 1951. R. M. Darnell and natives (field no. E-9). Repeat of collection 1A after week of heavy rains. CNHM colls.

Station 1C. April 20, 1951. R. M. Darnell and natives (field no. E-2). Second small spring above village of Encino and upper 15 m of creek. Water clear, current moderately slow; creek 1 m wide, 0-¼ m deep; bottom of shale and mud; little vegetation in water; partly shaded. Fishes collected by seine, and estimated half of population taken. CNHM colls.

Station 1D. April 20, 1951. R. M. Darnell and natives (field no. E-3). Lower 15 m of creek (down to its junction with the bed of the Arroyo Encino) above the village of Encino. Water clear, flowing; rock and mud bottom; 0–¼ m in depth; shaded by broad-leaved emergent plants (*Xanthosoma robustum*) growing in the water. Fishes collected by seine, and estimated one-fourth of population taken. CNHM colls.

Station 1E. April 20, 1951. R. M. Darnell and natives (field no. E-4). Pool of Arroyo Encino at mouth of spring creek above village of Encino. Water clear, current imperceptible; two bottom types evident: 1) rocks carpeted with filamentous algae and flocculent organic material (inhabited only by *M. sphenops*), and 2) exposed mixed bottoms of rocks, gravel, and sand (frequented by both *M. sphenops* and *G. regani*); pool about

TABLE 1

Fishes collected in the Arroyo Encino and Arroyo Sarco

	Arroyo Encino														Arroyo Sarco 2A	Per cent of total
	1A	1B	1C	1D	1E	1F	1G	1H	1I	1J	1K	1L	1M	1N		
Astyanax fasciatus	.....	.....	.....	.....	.....	41.7	16.0	6.8	.....	9.9	8.0	26.7	.....	.....	30.2	21.6
Dionda rasconis	.....	.....	.....	.....	.....	.....	1.2	17.4	.....	54.0	18.4	19.8	.....	.....	2.4	15.7
Dionda sp.	.....	.....	.....	.....	.....	.....	.....	.....	.....	1.4	1.2	6.7	.....	.....	.....	2.3
Notropis sp.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.6	8.9	.....	.....	.....	2.8
Ictalurus australis	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	(40.0)	.....	0.1
Gambusia regani	.....	27.3	11.5	60.0	22.9	.....	1.2	10.6	.....	1.7	0.6	1.2	.....	.....	3.9	3.9
Gambusia vittata	.....	.....	.....	.....	.....	.....	.....	.....	.....	21.5	31.9	15.8	.....	.....	.....	9.5
Mollienesia sphenops	.....	18.2	69.2	40.0	71.4	33.3	43.2	54.5	.....	7.2	26.4	13.7	.....	.....	43.4	30.0
Xiphophorus variatus	100.0	54.5	19.2	.....	5.7	.....	14.8	10.6	.....	1.4	8.6	2.4	(100.0)	.....	0.7	4.0
Cichlasoma cyanoguttatum	.....	.....	.....	.....	.....	25.0	22.2	.....	.....	2.2	1.2	1.6	.....	(20.0)	9.1	4.8
Cichlasoma steindachneri	.....	.....	.....	.....	.....	.....	1.2	.....	(100.0)	0.8	3.1	3.2	.....	(20.0)	10.4	5.2
Gobiomorus dormitor	.....	.....	.....	.....	.....	.....	.....	.....	.....	pv	pv	.....	.....	(20.0)	.....	0.1
Total no. in collection	9	11	26	5	140	12	81	132	(4)	363	163	899	(ca.12)	(5)	1,008	2,870

Figures represent the percentage composition of each collection. Bottom totals give numbers of fishes in each collection. Fishes not collected by seine are placed in parentheses. Sight records are recorded by the letter "p", and if the observation was later verified by specimens, it is marked "pv". Certain fishes taken by hook and spear are not included in the table but are discussed in the text.

6 m across and ⅓ m in depth; exposed, much sunlight. Fishes collected by seine, and estimated one-fifth of population taken. CNHM colls.

Station 1F. May 22, 1951. R. M. Darnell and natives (field no. E-10). Uppermost deep pool of Arroyo Encino at village of Encino (adjacent to and on both sides of bridge of Mexico-Laredo highway). Some human sewage in water. Dangerous collecting! Water turbid (black due to decomposing organic pollutants), no current; bottom of deep black mud containing much broken glass, cans, and other trash; 0–1½ m in depth; partly shaded. Fishes collected by seine. CNHM colls.

Station 1G. May 22 , 1951. R. M. Darnell and natives (field no. E-11). Arroyo of Encino 200 m below bridge of Mexico-Laredo highway. Much sewage from village of Encino floating in water. Water very turbid, no current; bottom deep organic ooze; 0–1 m in depth; enormous quantites of algae in water (chiefly *Spirogyra,* but also including *Merismopoedia, Oscillatoria, Mougeotia, Ulothrix,* and *Closterium*); many exogenous leaves and branches in water; partly shaded by moderately dense bank vegetation. Fishes collected by seine. CNHM colls.

Station 1H. May 8, 1950. R. M. Darnell and natives (field no. Sa-8). Pools in Arroyo Encino 200–400 m above junction with Río Sabinas (at least 3 km downstream from Station 1G). Water slightly turbid, current very slow; rocky bottom carpeted with some mud and much flocculent organic material (containing diatoms, filamentous algae, and decomposing vegetation); depth 0–1 m; some vegetation in shallows; partly shaded; arroyo bed deep here, bank steep and heavily vegetated on north side, low and sparsely vegetated on south side. Fishes collected by seine. CNHM Colls.

Station 1I. April 17, 1951. R. M. Darnell and natives (field no. E-5). Pool in Arroyo Encino 200 m above junction with Río Sabinas. Habitat data same as for Station 1H. Observations on apparent nest-building behavior of *C. steindachneri.* Fishes collected by length of gill net employed as seine. CNHM colls.

Station 1J. May 2, 1950. R. M. Darnell and natives (field no. Sa-7). Pools in lower 200 m of Arroyo Encino at junction with Río Sabinas. Habitat data approximately as in 1H, although pools slightly deeper, and the mouth of the Arroyo is essentially a long, deep, quiet backwater of the Río Sabinas. Steep banks were densely vegetated. Fishes collected by seine. CNHM colls.

Station 1K. April 28, 1950. R. M. Darnell and natives (field no. Sa-4). Same as 1J except that only lower 150 m of Arroyo were included. Fishes collected by seine. CNHM colls.

Station 1L. December 21, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field nos. X-2, 3, 4, 5, 6). Repeat of 1J, except that some gravel riffles were included. Fishes collected by seine. Mus. nos. TU 5574–83.

Station 1M. January 2–3, 1951. R. M. Darnell (field no. X-30). Collection made in backwater behind log in second pool above mouth of Arroyo Encino. Live fishes (*X. variatus* only) collected in overnight set of a glass minnow trap. Fish brought back alive for experimentation.

Station 1N. January 3, 1951. R. M. Darnell (field nos. X-29, 31). Mouth of Arroyo Encino. Conditions as described in 1J. Fishes collected by fyke nets. Mus. nos. TU 5691–94.

Series 2. Arroyo Sarco (tributary of Arroyo Encino). Pond series about 2 km northeast of Storms' Ranch.

Station 2A. December 23, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field nos. X-7, 8, 9, 10, 11). Collections made from a series of ponds connected by a small trickle of water which disappeared underground at the lower pond. Water clear; bottoms variable, rock, mud; 0–1 m in depth; some ponds with much emergent vegetation, others with thick floating mats of filamentous algae; shore composed of exfoliating shale and surrounded by scrub vegetation. Fishes collected by seine. Mus. nos. TU 5584–90.

Series 3. Arroyo La Flor. Pond series from Nacimiento of Río Sabinas north in the arroyo for about ½ km. Conditions variable from one pond to another and from one season to another within a given pond.

Station 3A. January 1, 1953. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-28). Uppermost (6th) pond above Nacimiento of Río Sabinas. Water clear, basin rocky; 0–2 m in depth; little aquatic vegetation except algae carpeting some rocks; shore rocky and slightly wooded. Fishes collected by seine. Mus. nos. TU 5686–90.

Station 3B. December 24, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field nos. X-16, 17, 18). Upper (4th and 5th) ponds and broad, shallow, interconnecting riffle above Nacimiento of Río Sabinas. Water mostly clear; basin of rock and gravel; 0–1 m in depth; much matted green algae, especially in riffle, rocks coated with algae; shore a rocky beach with occasional trees. Fishes collected by seine. Mus. nos. TU 5603–07.

Station 3C. December 23, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field nos. X-13, 14, 15). Lower (1st, 2nd, and 3rd) ponds above Nacimiento of Río Sabinas. Water clear, slight current; basin of limestone rock and boulders; 0-1 m in depth; rocks coated with algae; shore of rock and boulders. Fish collected by seine, but one large catfish (*I. australis*) sought shelter in crevice under boulder and was extracted by hand. Mus. nos. TU 5594–5602.

Station 3D. April 29, 1951. R. M. Darnell and natives (field no. E-7). First pond above Nacimiento of Río Sabinas. Water clear, without perceptible current (the fishes had probably been isolated for 5–6 months previous); 0–1 m deep; basin of limestone bedrock; some algae coating rock; shore of rock and boulders. Fish collected by seine. CNHM colls.

Series 4. Río Sabinas—river series from Nacimiento to junction with Río Guayalejo.

Station 4A. April 30, 1950. R. M. Darnell and natives (field no. Sa-6). Former bed of Río Sabinas which forms a long, shallow extension of the Nacimiento (est. 40 m × 4 m) parallel to Río Sabinas at its origin and connected with Río Sabinas for about 10 m. Water clear, current moderate in initial 10 m, but virtually absent in remaining pocket; basin of limestone and conglomerate rocks, mostly covered by silt, mud, or ooze; depth 0–1 m; rooted aquatic plants and algae mats abundant; shore rocky and exposed. Fishes collected by seine. CNHM colls.

Station 4B. April 29, 1951. R. M. Darnell and natives (field no. E-6). Repeat of 4A. Fishes collected by seine. CNHM colls.

Station 4C. December 23, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-12). Repeat of 4A. Fishes collected by seine. Mus. nos. TU 5591–93.

Station 4D. April 13, 1950. R. M. Darnell and B. E. Harrell (field no. Sa-3). Shallow backwater of Río Sabinas 200 m upstream from Storms' Ranch. Water slightly turbid, no current; bottom of rock, gravel, sand, and silt, generally covered with a layer of organic detritus; depth 0–½ m, but mostly less than 5 cm; shallow water heavily coated

TABLE 2

Fishes collected in the Arroyo La Flor and Río Sabinas
(For explanation see Table 1)

	Arroyo La Flor				Río Sabinas												
	3A	3B	3C	3D	4A	4B	4C	4D	4E	4F	4G	4H	4I	4J	4K	4L	Per cent of total
Astyanax fasciatus	16.2	17.7	22.3	62.3	60.2	49.8	11.4	6.8	22.0	14.4	15.4	1.4	62.7	3.6	13.3	3.4	20.7
Ictiobus bubalus (?)	.....	.....	.....	.....	p	.....	.....	p	.....	.....	.....	.....	.....	.....	.....	.....	p
Dionda rasconis	78.2	53.5	13.8	.....	.....	0.4	.....	35.3	26.6	15.2	15.4	86.4	19.6	31.0	47.1	28.2	27.0
Dionda sp.	.....	.....	.....	.....	.....	.....	.....	1.5	2.5	7.2	.....	.....	.....	.....	2.9	1.9	0.7
Notropis lutrensis	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.7	.....	2.0	2.9	15.3	1.4
Notropis sp.	.....	.....	.....	.....	.....	.....	.....	6.0	.....	2.4	.....	.....	2.0	.....	1.0	1.5	0.5
Ictalurus australis	.....	.....	0.1	.....	p	.....	.....	pv	pv	.....	pv	.....	.....	.....	.....	.....	0.1
Gambusia regani	.....	.....	0.5	0.9	1.9	1.7	.....	.....	.....	15.2	15.4	.....	.....	2.8	2.4	3.8	1.5
Gambusia vittata	.....	.....	.....	.....	.....	.....	.....	34.6	36.1	25.6	.....	11.4	13.7	35.7	20.0	40.1	11.3
Mollienesia sphenops	3.5	8.6	61.6	25.4	11.7	7.7	77.1	9.0	2.9	20.0	38.5	.....	.....	6.0	1.0	3.4	28.7
Xiphophorus montezumae	.....	.....	0.1	0.9	26.2	19.6	.....	.....	0.8	.....	.....	.....	.....	.....	.....	.....	2.0
Xiphophorus variatus	.....	.....	0.1	.....	.....	.....	.....	.....	2.9	.....	.....	.....	.....	.....	4.3	0.8	0.5
Agonostomus monticola (?)	p	.....	.....	.....	p	p	.....	p	p	.....	p	.....	.....	.....	.....	.....	p
Cichlasoma cyanoguttatum	0.7	0.5	0.5	10.5	p	7.7	.....	p	1.7	.....	p	.....	.....	.....	0.5	.....	1.2
Cichlasoma steindachneri	1.4	19.7	1.0	.....	.....	13.2	11.4	6.8	4.6	.....	15.4	.....	2.0	18.7	4.8	1.5	4.6
Gobiomorus dormitor	.....	.....	.....	.....	.....	.....	.....	p	.....	.....	pv	.....	.....	0.4	.....	.....	0.1
Total no. in collection	142	198	1,481	114	103	235	70	133	241	125	13	280	51	252	210	262	3,910

(?) = records in need of verification (see text).

with floating mats of filamentous green algae; bank heavily vegetated on one side, partly shaded. Fishes collected by seine. CNHM colls. Note: Day and night observations as well as collections made by hook and spear in adjacent deep water indicated the presence of several species not captured here in the seines. These are indicated simply as present (p). On May 10th a young Fer-de-lance, *Bothrops atrox* (130 cm), was captured about fifty meters downstream from this station on the heavily vegetated riverbank two meters from the water's edge at the terminus of a trot line. This marks the approximate northern limit of distribution of this deadly snake.

Station 4E. April 28, 1950. R. M. Darnell and natives (field no. Sa-5). Río Sabinas at Storms' Ranch. Entire downstream edge of long pool which receives mouth of Arroyo Encino. Collections made at night (9:30—10:30 p.m.). Water slightly turbid, slight current; mixed bottom of rocks, gravel, sand, silt, mud, and ooze; depth 0–1½ m, collections made through a thick growth of vegetation, mostly *Potamogeton;* bank exposed, but no light at night. Fishes collected by seine. CNHM colls.

Station 4F. December 21, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-1). Repeat of 4E except that collections were made during afternoon. Fishes collected by seine. Mus. nos. TU 5567–73.

Station 4G. April 2 1950. R. M. Darnell and natives (field no. Sa-1). Río Sabinas at Storms' Ranch, 200 m downstream from 4E. Collections made at edge of pool just below extensive riffle. This collection represents normal condition at the end of the dry season. Water clear, edge of moderate current; bottom of sand, rock, and gravel; depth 0–1 m; vegetation absent; water shaded. Fishes collected by seine. CNHM colls.

Station 4H. April 8, 1950. R. M. Darnell and natives (field no. Sa-2). Location same as 4G. Depth 0–15 cm. Fishes collected by means of a length of window screening. Screen was fanned just above bottom, creating a patch of turbid water, then raised to capture the fishes attracted by the suspended matter. CNHM colls.

Station 4I. May 12, 1950. R. M. Darnell and natives (field no. Sa-9). Repeat of 4G after series of heavy rains. Current very swift. Fishes collected by seine and were probably not in the full current. CNHM colls.

Station 4J. May 26, 1950. R. M. Darnell and natives (field no. Sa-10). Repeat of 4G and 4I after water level was back to normal. Water clear, current slight; bottom heavily silted. Fishes collected by seine. CNHM colls.

Station 4K. April 30, 1951. R. M. Darnell and natives (field no. E-8). Río Sabinas at Rancho Pico de Oro (3½ km northeast of Gomez Farías, Tamps., Mexico). Backwater and pool collections. Water clear, edge of moderate current; bottom of sand, silt, mud with many exogenous leaves; depth 0–1 m; vegetation sparse; water shaded by trees growing on rocky beach; 100 m upstream the dense forest extends to water's edge and dense stands of aquatic vegetation are present in water. Fishes collected by seine. CNHM colls.

Station 4L. January 1, 1953. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-27). Río Sabinas under bridge of Mexico-Laredo highway (km #595.5) (6 km southeast of Gomez Farías, Tamps., Mexico). Collections made from edge of long pool. Water clear; current slow; bottom varied, rocks, gravel, sand, mud; depth 0–1 m; aquatic vegetation in part of area seined; water shaded by bridge and by high trees on floodplain. Fishes collected by seine. TU 5676–85.

Series 5. Río Frío series below Nacimiento.

Station 5A. December 31, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-25). Pool of Río Frío at meteorological station near Nacimiento (about 6 km south of Gomez Farías, Tamps., Mexico). Water clear, current slight; bottom mud and gravel; 0–1 m in depth; much aquatic vegetation around margin; water shaded by shore trees. Fishes collected by seine. TU 5662–68.

TABLE 3

Fishes collected in the Río Frío and Río Boquilla
(For explanation see Table 1)

	Río Frío	Río Boquilla					
	5A	6A	6B	6C	6D	6E	Per cent of total
Dorosoma cepedianum	...	...	0.6	..	2.5	1.4	1.4
Astyanax fasciatus	19.3	5.8	2.9	15.0	28.7	1.8	16.4
Dionda rasconis	...	.....	4.9	14.8	20.4	13.5	14.2
Dionda sp.	45.7	.....	....	.....		.....	3.0
Ictalurus australis	.....	.....	1.2	1.3	0.9	.....	0.8
Ictalurus furcatus	.....	.....	.....	.....	1.3	.	0.5
Gambusia panuco	.....	55.7	20.7	6.2	7.4	0.8	8.2
Gambusia vittata	16.7	.. .	.	.. .	.		1.1
Mollienesia sphenops	1.2	19.2	59.7	59.6	22.9	20.5	32.5
Xiphophorus montezumae	4.8	.....	.....	.....	. . .	.....	0.3
Xiphophorus variatus	10.2	1.9	...	. . .	3.1	.....	2.0
Cichlasoma cyanoguttatum	.....	17.3	9.8	3.1	12.6	62.0	19.5
Cichlasoma steindachneri	1.8	.....	0.3	.....	0.1	.....	0.2
Total no. in collection	166	52	347	453	1023	497	2,538

Series 6. Río Boquilla series (R. Frío drainage)—river and tributaries in Chamal valley.

Station 6A. December 26, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-22). Spring pool in headwaters of Río Boquilla on Ben Gorham ranch (about 2 km west of Chamal, Tamps., Mexico). Water slightly turbid, current imperceptible; bottom mud; 0–1 m in depth; aquatic vegetation sparse; water shaded. Fishes collected by seine. Mus. nos. TU 5628–5632.

Station 6B. December 26, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-21). Shallow arroyo pools in headwaters of Río Boquilla (about 2 km southeast of Chamal, Tamps., Mexico). Water slightly turbid; current slight; bottom of mud, rocks, and gravel; 0–½ m in depth; aquatic vegetation limited to algae on rocks; partly shaded. Fishes collected by seine. Mus. nos. TU 5620–27.

Station 6C. December 26, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-19). Deep pool in Río Boquilla at mouth of arroyo on Jorilla ranch (6.4 km southeast of Chamal, Tamps., Mexico). Water fairly turbid, no current; bottom of mud, rocks, and gravel; 0–2 m deep; aquatic vegetation absent; water partly shaded. Fishes collected by seine. Mus. nos. TU 5608–13.

Station 6D. April 5, 1950. R. M. Darnell and B. E. Harrell (field no. Ch-1). Collections made at end of long, exceptionally dry season from a series of deep pools in bed of Río Boquilla on Procter ranch (3 km east of Chamal, Tamps., Mexico). Water very turbid, no current; bottom of fine silt and mud; 0–2 m deep; no vegetation, but much brush and logs in water; shaded. Fishes collected by seine. CNHM colls.

Station 6E. December 26, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field

no. X-20). Shallow lake in headwaters of Río Boquilla on ranch of Don Modesto (about 4 km southeast of Chamal). Water turbid, no current; muddy bottom; 0–1½ m deep; vegetation scarce; exposed. Fishes collected by seine. Mus. nos. TU 5614–19.

Series 7. Río Mante series, irrigation ditch and river from Nacimiento to below reservoir.

TABLE 4

Fishes collected in the Río Mante
(For explanation see Table 1)

	Irrigation ditch	Río Mante			
	7A	7B	7C	7D	Per cent of total
Astyanax fasciatus	1.0	7.3	8.1	14.4	11.0
Dionda sp.	10.3	.....	.....	1.3	1.6
Gambusia affinis	.....	0.9	1.0	13.6	8.3
Gambusia vittata	52.6	47.7	2.0	24.2	30.7
Gambusia sp.	.....	.....	.....	0.9	0.6
Mollienesia latipunctata	32.0	11.5	82.9	42.0	36.5
Mollienesia sphenops	4.1	28.1	1.0	3.5	9.8
Cichlasoma cyanoguttatum	.....	1.2	.....	.....	0.3
Cichlasoma steindachneri	.....	3.3	5.0	0.1	1.3
Gobiomorus dormitor	.....	.....	.....	pv	p
Total no. in collection	97	331	99	745	1,272

Station 7A. June 4, 1950. R. M. Darnell and natives (field no. Ma-3). Roadside ditch and concrete culvert midway between Ciudad Mante and reservoir (about 3 km southwest of Ciudad Mante, Tamps., Mexico). Water clear, moderate current; bottom of mud and concrete; depth 0–1½ m; vegetation dense in ditch, but limited to encrusting algae on aprons of culvert; exposed. Fishes collected by seine. CNHM colls.

Station 7B. January 1, 1953. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-26). Small pools and riffles of Río Mante 200 m below dam (about 4 km southwest of Ciudad Mante). Water clear, current slow; bottom of rocks, gravel, and mud; depth 0–½ m; vegetation absent; partly shaded. Fishes collected by seine. Mus. nos. TU 5669–5675.

Station 7C. May 3, 1950. R. M. Darnell and B. E. Harrell (field no. Ma-1). Collections from edge of Río Mante 100–200 m below its Nacimiento on the Rancho Río Escondido (about 8 km southwest of Ciudad Mante). Water clear, current slow but definite; bottom of mud; depth 0–1½ m; submerged vegetation (*Myriophyllum*) very dense; partly shaded. Fishes collected by seine. CNHM colls.

Station 7D. June 4, 1950. R. M. Darnell and natives (field no. Ma-2). Collections from flooded beach at edge of reservoir of Río Mante, 100–200 m above dam (4 km southwest of Ciudad Mante). Water clear although surface covered with floating straw, no perceptible current; bottom of soil and grass (flooded); depth 0–1½ m; vegetation grass and weeping willow tree branches in water; exposed. Fishes collected by seine. CNHM colls.

Series 8. Río Guayalejo series—from Forlón to mouth of Río Sabinas.

Station 8A. May 10, 1903. S. E. Meek (no field no.). Río Guayalejo, about 30 km southeast of Llera and about 30 km northeast of Xicotencatl. The following quotations are taken directly from Meek's field notes relating to May 9 and 10, 1903. "Went to ranch of Graham and Hudson." "River at buildings, about 50 feet below, Bottom of

TABLE 5

Fishes collected in the Río Guayalejo
(For explanation see Table 1)

	Río Guayalejo	
	8A	8B
Lepisosteus osseus	X	0.5
Dorosoma cepedianum	X	..
Astyanax fasciatus	X	17.2
Ictiobus bubalus	X	
Dionda rasconis	X	15.8
Dionda sp.		2.7
Notropis lutrensis	X	7.7
Notropis sp.		20.4
Ictalurus australis	X	15.4
Ictalurus furcatus	....	2.7
Ictalurus mexicanus	...	1.4
Gambusia regani	X(H)	(?)
Gambusia vittata	X(H)	3.2
Mollienesia formosa	..	0.5
Mollienesia latipunctata	X	..
Mollienesia sphenops	X	7.2
Xiphophorus variatus	X	.....
Cichlasoma cyanoguttatum	X	4.1
Cichlasoma steindachneri	X	0.9
Gobiomorus dormitor	X	0.5
Total no. in collection	....	221

X = present in Meek's collection.
X(H) = presence in Meek's collection established by Hubbs (1926).
(?) = identification questionable.

river stony, current swift. river varies from 40 to 75 feet wide, Fishes not collected are the Roballo, long nosed gar, one of which I saw in the water, and the fresh water drum, ..." In his publication Meek (1904) mentioned that during the dry season the river was a small stream flowing over a "rocky and gravelly bed," and he further reported seeing longnose gars in "a deep sluggish creek at Forlón." Fishes probably collected by seine. Mus. nos. CNHM 4474–90, 14033–58, 15592–16647.

Note: Most maps of this area show two neighboring localities with the name of Forlón, one on the railroad and the other on the Río Guayalejo about 6 km south of the first. Neither locality has been visited by the present writer. Meek's description is about what would be expected for the Río Guayalejo midway between Xicotencatl and Llera during early May, however, and since no other major tributary is known in that area with fifty foot high banks and with swift water during the dry season, it is tentatively assumed that his collecting station was located in the southernmost of the two Forlóns on the Río Guayalejo.

Station 8B. December 31, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-24). Río Guayalejo at Adjuntas, across from mouth of Río Sabinas (7 km southwest of Xicotencatl). Water turbid, current moderate to swift; bottom of rock, covered in some places with silt; depth 0–1½ m; aquatic vegetation absent; exposed. Fishes collected by seine. Mus. nos. TU 5646–61.

Series 9. Río Tamesí and lagoons around Tampico.

Station 9A. Unspecific records from the Tampico area ("Tampico", "Tampico fish market", "lagoon(s) at Tampico", "lagoon near Tampico", "coastal lagoons", "lagoon near mouth of Río Pánuco", "the river") by various authors (Duméril, 1870; Jordan

TABLE 6

Fishes recorded from the Tampico area or collected from the Laguna de Chairel
(For explanation see Table 1)

	"Tampico"	Laguna de Chairel
	9A	9B
Carcharhinus leucas	X	.....
Lepisosteus osseus	X	.....
Lepisosteus spatula	X	.....
Anchoa hepsetus	(?)	.....
Anchoa mitchilli	X	0.4
Dorosoma cepedianum	X	15.6
Dorosoma petenense	....	23.4
Astyanax fasciatus	X	.....
Ictiobus bubalus	X	.....
Galeichthys felis	X	..
Ictalurus furcatus	X	.. .
Oostethus lineatus	X	.....
Cyprinodon variegatus	(?)	.....
Fundulus grandis	(?)	.....
Fundulus similis	(?)	.....
Lucania parva	...	0.8
Gambusia affinis	X	0.8
Mollienesia latipinna	X	.....
Mollienesia sphenops	X	.....
Mugil cephalus	X	0.4
Mugil curema	X	0.4
Caranx hippos	X	.....
Caranx latus	....	2.5
Lutjanus cyanopterus	X	.....
Lutjanus griseus	X	.....
Archosargus probatocephalus	X	.....
Eugerres brasilianus	X	.....
Eugerres plumieri	X	.....
Eucinostomus melanopterus	X	4.9
Bairdiella ronchus	X	.....
Cynoscion nebulosus	X	.....
Micropogon undulatus	X	.....
Pogonias cromis	X	.....
Chaetodipterus faber	X	.....
Cichlasoma cyanoguttatum	X	36.1
Cichlasoma steindachneri	....	5.7
Dormitator maculatus	..	8.2
Eleotris pisonis	X	.....
Gobiomorus dormitor	X	0.8
Evorthodus lyricus	X	.....
Gobionellus boleosoma	X	.....
Gobionellus claytoni	(?)	.....
Gobiosoma bosci	(?)	.....
Citharichthys spilopterus	X	.....
Opsanus beta	(?)	.....
Total no. in collection	....	244

(?) = records in need of verification (see text).

and Snyder, 1901; Meek, 1904; Jordan and Dickerson, 1908; Regan, 1908, 1913).

Station 9B. December 29, 1952. R. M. Darnell, J. H. Darnell, and E. Liner (field no. X-23). Laguna de Chairel at Tampico (shore of island across lagoon from Balneario Rojas). Several collections made around island including drags to the muddy shore as well as purses of seine in areas where the shore was unapproachable. Water moderately turbid, not salty to taste (est. 1–4 ‰ salinity), no current; mud bottom; depth 0–2 m; many beds of aquatic vegetation, also clear areas; shore conditions variable, including

sedge mat, marsh, and mud beach; exposed. Fishes collected by several sizes of seines. Mus. nos. TU 5633–45.

Annotated List of Species

CARCHARHINIDAE—Requiem Shark Family

Carcharhinus leucas (Müller and Henle). Bull shark

Carcharias platyodon (Poey). Jordan and Dickerson (1908, Tampico)

Carcharhinus leucas (Müller and Henle). Baughman and Springer (1950, Tampico)

Atlantic coast of Americas from New York to Brazil; also in Bermuda and West Indies.

The bull shark is a frequent visitor of brackish water lagoons on the northern Gulf coast (Darnell, 1958; Hoese, 1958), and it has been known to penetrate rivers as much as 160 miles from the mouth (Gunter, 1938). Although no specimens were taken in the present study, the species is anticipated from the Tampico lagoons. The closely related *C. nicaraguensis* inhabits fresh water. Food habits of the bull shark on the northern Gulf coast have been summarized by Darnell (1958), and Baughman and Springer (1950) have discussed breeding habits of the species.

Station: 9A.

LEPISOSTEIDAE—Gar Family

Lepisosteus osseus (Linnaeus). Longnose gar, "Aguja"

Lepisosteus osseus (Linnaeus). Jordan and Snyder (1901, Tampico)

Lepidosteus osseus (Linnaeus). Meek (1904, San Juan, Valles, Forlón)

Eastern United States; along Atlantic and Gulf coasts from Massachusetts south to the Río Pánuco.

Jordan and Snyder (1901) reported that the longnose gar was plentiful in Tampico markets and that these specimens were said to have been taken from the "river and neighboring lagoons."

Although he captured no specimens of the longnose gar in the Tamesí, Meek (1904) reported seeing a number of them in a deep sluggish creek at Forlón. In the present study a single small specimen was taken from the Río Guayalejo at Adjuntas.

The longnose gar is undoubtedly widely distributed throughout the deeper waters of the Tamesí drainage which have not been adequately sampled. On the northern Gulf coast the species has been taken from brackish waters (Darnell, 1958), and even though it may occur in the brackish lagoons around Tampico, it is probably not as characteristic of these lagoons as is the more euryhaline alligator gar. In the headwater tributaries the natives recognize the longnose gas as the "aguja" and state that it is an occasional visitor in the Río Sabinas at least as far up as Storms' Ranch.

This species is a predator on fishes and larger invertebrates, and its food habits on the northern Gulf coast have recently been discussed by Darnell (1958).

Stations: 8A, 8B, 9A.

Museum No.: TU 5646.

Lepisosteus spatula (Lacépède). Alligator gar, "Catán"

Atractosteus lucius Duméril. Duméril (1870, Tampico)

Lepisosteus tristoechus (Bloch and Snyder). Jordan and Snyder (1901, Tampico)

Lepidosteus tristoechus (Bloch and Snyder). Meek (1904, Tampico)

Streams of southeastern United States draining into the Gulf of Mexico and coastal lagoons south to Tampico, Vera Cruz, Mexico.

Meek (1904) indicated the presence of the alligator gar in the markets where it is sold for food, and he mentioned that this fish is reported to be quite abundant in the large river channels and lagoons about Tampico. No specimens of the alligator gar were taken in the present study.

In southern Texas Gunter (1945) captured the alligator gar in waters of nearly marine salinity, although he stated that the species probably prefers waters of low salinity. Natives of the headwaters are familiar with the species, calling it the "catán", but they indicated that this fish does not normally enter the shallow headwater streams. Food habits of the alligator gar on the northern Gulf coast have recently been discussed by Darnell (1958).

Station: 9A.

ENGRAULIDAE—Anchovy Family

Anchoa hepsetus (Linnaeus). Striped anchovy

Anchovia brownii (Gmelin). Jordan and Dickerson (1908, lagoon at Tampico)

Along the Atlantic coast from Nova Scotia to Uruguay; also in the West Indies.

The presence of the striped anchovy in the Tampico lagoons is highly likely, since it has been reported from bays and estuaries both above and below the Tampico area (see, for example, Hubbs, 1936; Gunter, 1945; Hoese, 1958). This anchovy feeds on small crustaceans, mainly copepods, and small bottom animals (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1930). On the North Carolina coast it apparently begins spawning slightly earlier than does *A. mitchilli* (Hildebrand and Cable, 1930).

Station: 9A.

Anchoa mitchilli (Valenciennes). Bay anchovy

Anchovia mitchilli (Cuvier and Valenciennes). Jordan and Dickerson (1908, lagoon near Río Pánuco)

Bays and lagoons of eastern North America from Maine to Yucatán.

In the present study a single specimen was taken from the Laguna de Chairel, confirming the presence of the bay anchovy in the Tampico area, and indicating its penetration of the fresher lagoons. As pointed out by Gunter (1945) the bay anchovy is euryhaline, and, although it has been reported to enter streams, it is normally encountered in brackish to marine waters.

Food studies of northern Gulf populations were reported by Darnell (1958).

Stations: 9A, B.

Museum No.: TU 5635.

CLUPEIDAE—Herring Family

Dorosoma cepedianum (LeSueur). Gizzard shad

Dorosoma exile Jordan and Gilbert. Meek (1904, San Juan, Valles, Forlón)

Dorosoma cepedianum (LeSueur). Jordan and Dickerson (1908, lagoon near Tampico)

Eastern United States; coastal streams and lagoons from Massachusetts south to the Río Pánuco.

In the present study 35 specimens of this fish were obtained from the Río Boquilla and its tributaries in the headwaters of the Tamesí, and 38 specimens were seined from the Laguna de Chairel at Tampico. The headwater specimens were taken from an arroyo, a small lake, and from pools of the Río Boquilla from two to six feet in depth. No specimens were obtained from other headwater streams or from the Río Guayalejo at Adjuntas where the current was moderate to swift.

Future collecting will probably reveal that this species is found throughout the fresh and brackish waters of the Tamesí drainage in pool and lake-like environments which are characterized by some turbidity, little or no current, and mud or silt bottoms. It is known to be a resident of brackish waters on the northern Gulf coast. As pointed out by Hubbs, Kuehne, and Ball (1953) the gizzard shad is not readily taken in small seines, hence the species may be more widely distributed in the headwaters of the Tamesí than presently indicated.

Food habits of the gizzard shad on the northern Gulf coast have recently been summarized by Darnell (1958). Stomachs of five specimens from the Río Boquilla were examined, and all were found to contain great quantities of finely-powdered silt. Several of the individuals had consumed large numbers of minute eggs of undetermined origin as well as occasional specimens of *Difflugia sp.*

Stations: 6B, 6D, 6E, 8A, 9B.

Museum Nos.: CNHM 4481, 62642; TU 5614, 5621, 5645.

Dorosoma petenense (Günther). Threadfin shad

Signalosa mexicana (Günther). Meek (1904, Valles)

Gulf of Mexico and coastal lagoons from Florida west through Texas and south to British Honduras.

In the present study 57 specimens were taken from the Laguna de Chairel at Tampico, but the species did not appear in any of the other collections from the Tamesí drainage. The presence of this shad in Meek's collection from Valles, many miles from the Gulf, suggests that it may also be present in the larger streams and possibly in the headwaters of the Río Tamesí, even though it has not yet been collected there. Like the gizzard shad this species is not readily taken in small seines. The threadfin shad is known to have wide tolerance for salinity, and Gunter (1956) considered the species to be anadromous.

On the basis of limited published information, the threadfin shad is considered to be a plankton feeder, although some bottom feeding may also take place (Darnell, 1958). The taxonomic position of the threadfin shad has recently been discussed by Bailey *et al* (1954).

Station: 9B.

Museum No.: TU 5642.

CHARACIDAE—Characin Family

Astyanax fasciatus (Cuvier). Banded tetra

Tetragonopterus mexicanus Filippi. Jordan and Snyder (1901, Rio Axtla), Meek (1904, Forlón, Valles, Rascón)

Tetragonopterus argentatus (Baird and Girard). Jordan and Snyder (1901, Río Verde)

Astyanax argentatus Baird and Girard. Jordan and Dickerson (1908, lagoon near Tampico)

Astyanax fasciatus (Cuvier). Miller (1956, La Media Luna)

Coastal streams from southern and western Texas to South America.

In the present study 2,025 specimens were obtained, and this fish was present in every collection made from the Ríos Sabinas, Frío, Boquilla, Mante, and Guayalejo. It was also represented in every seine collection from the Arroyo Encino except those from the very shallow springs and spring creek. Surprisingly, the species was not obtained from the Laguna de Chairel at Tampico. The banded tetra is widely distributed throughout the headwater tributaries of the Río Tamesí system. It is probably found in the larger river, and the collections of Jordan and Dickerson (1908) demonstrate that this fish is also present in some of the coastal lagoons.

The banded tetra is one of the most abundant species of fish in the headwaters of the Tamesí. Although it was found to be present in almost every available habitat type, the species was generally not abundant in very swift water, very shallow creeks, or lake-like areas. It is primarily an inhabitant of deep river pools and moderately shallow backwaters with some current. In the deeper clear, slow-flowing pools of the Río Sabinas around Storms' Ranch this species was very abundant, and it was frequently observed swimming at any depth (down to 3 m), either singly or in tight schools of fifty or more individuals. These fish quickly investigated any disturbance of the water surface. At night this characin remained quiet in the deeper pools. The habitat of the banded tetra overlapped that of *C. cyanoguttatum*, and the two species were often observed together in mixed schools. Due to the wariness of the latter species, however, the seining data do not adequately reflect the association of the two species.

Stomach contents of twenty-one individuals were examined, and the food of this characin was found to be quite variable. Vegetation made up 62 per cent of the food, animal matter made up 22 per cent, and detritus constituted the remainder. Most of the vegetation was filamentous algae (*Spirogyra*, *Rhizoclonium*, *Oscillatoria*, and *Hyalotheca*), although some fungus and green leaf fragments also were present. The filamentous algae were consumed in parallel sheaves which were clipped in bunches and tamped at the ends like elongated shredded wheat biscuits. Each "biscuit" was around five millimeters in length and contained about 55 strands of algae. About fifty such "biscuits" were required to fill the stomach of a single fish. Most of the animal matter consisted of aquatic insects (Coleoptera, Diptera, Homoptera, Odonata, and Trichoptera), as well as some of terrestrial origin, and one fish contained at least twenty different insects. Fish eggs and fish larvae were found in the stomachs of two individuals, one of which had consumed a total of twenty-four fish eggs. This little fish has wide food tolerances, and the frequency of utilization of each type of food is probably related to the availability of the food in the particular habitat.

Meek (1904) suggested that spawning takes place in the latter part of May and early June. Information obtained by the present writer, however, indicates that in the Río Sabinas spawning probably begins no earlier than mid-June. Although females collected in April possessed mature eggs, on June 7th thousands of adult characins were observed schooling in an area of about twenty square meters at the head of navigation where the Arroyo La Flor enters the Nacimiento. These fishes were not spawning, but they apparently were awaiting rains to afford them passage further up the Arroyo

La Flor where spawning must occur. The ripe ovary of a moderate-sized adult female contained about 1,500 eggs of small size (ca. 0.8 mm in diameter).

Stations: 1F–H, J–L; 2A; 3A–E; 4A–L; 5A; 6A–E; 7A–D; 8A, B.

Museum Nos.: CNHM 4480, 62643, 62652, 62664, 62672; TU 5569, 5583, 5590, 5591, 5599, 5606, 5608, 5616, 5622, 5628, 5657, 5666, 5670, 5685, 5690.

CATOSTOMIDAE—Sucker Family

Ichtiobus bubalus (Rafinesque). Smallmouth buffalo, "Boquin"

Carpiodes tumidus Baird and Girard. Jordan and Snyder (1901, Tampico Lagoons) Meek (1904, Forlón)

Ictiobus tumidus (Baird and Girard). Regan (1908)

Ictiobus bubalus (Rafinesque). Hubbs (1930)

Larger rivers and lakes from Canada and eastern United States south to the Río Tamesí.

During the present study no suckers were captured although they were frequently observed. One large sucker was often seen in the depths of the Nacimiento of the Río Sabinas. On several occasions in late May a group of suckers was observed in the Río Sabinas a few hundred meters above Storms' Ranch where they congregate, apparently awaiting higher water from the spring rains for upstream passage of shallow riffles. Two large specimens which had been speared from this group by the natives were examined briefly by the writer after they had been partially prepared for cooking. These specimens were identifiable to genus but not to species. Both were ripe females. Another sucker, *Ictiobus labiosus* (Meek), has been recorded from the drainage of the Río Pánuco, and this species may also be present in the Río Tamesí.

Stations: 8A, 9A.

Museum No.: CNHM 4476.

CYPRINIDAE—Minnow Family

Dionda rasconis (Jordan and Snyder).

Notropis rasconis Jordan and Snyder. Jordan and Snyder (1901, Rio Verde, Rascón)

Hybognathus rasconis (Jordan and Snyder). Meek (1904, Río Pánuco)

Dionda rasconis (Jordan and Snyder). Miller (1956, Río Verde, La Media Luna)

Endemic to the Pánuco-Tamesí drainage system.

In the present study 1,904 specimens were taken. This fish was found to be abundant in collections from the Arroyo Encino and the Ríos Sabinas, Boquilla, and Guayalejo. It was entirely absent from the Río Mante collection, being partially replaced by *Dionda sp.*, and it was not obtained from the Laguna de Chairel at Tampico. This minnow is widespread and abundant in most headwater tributaries of the Tamesí system, and it may be present in the larger rivers, as well. Moore (1957) put forth reasons for separating *Dionda* from *Hybognathus*, and Clark Hubbs and Brown (1956) discussed the status and relationships of the three described species of the genus *Dionda*.

D. rasconis inhabits shallow backwater and pool areas and is often associated with weed beds. It was abundant in many areas of the Río Sabinas at the edge of the main current, but it appeared equally successful in isolated pools of the arroyos and the

Río Boquilla without current. This species also frequented shallow gravel riffles where the current was slow. Mud or silt bottoms appeared to be important, and the absence of suitable bottoms may have been responsible for the apparent absence of this fish from the uppermost reaches of the Arroyo Encino, Nacimiento of the Río Sabinas, the Río Frío, the spring pool of the Río Boquilla, and the Río Mante.

The stomachs of 20 specimens were examined and all contained food. Arthropod remains (insects and water mites) made up about one-fifth of the stomach contents. Bits of filamentous algae and occasional diatoms made up about one-tenth, and the remaining material was bottom detritus and such matter as would be consumed with the detritus. It is obvious that this minnow feeds primarily upon detritus gleaned from the surface of the bottom. In the process it also ingests sand grains, bottom diatoms (*Navicula, Pinnularia, Sirurella*, etc.), scraps of filamentous algae (*Aphanizomenon, Lyngbya, Rhizoclonium*), desmids (*Micrasterias*), and bits of fungi and vascular plant matter. The presence of numerous small arthropods suggests some selectivity in feeding. This minnow is one of the several species which nip at bathers in the river. Great numbers of young were attracted to the turbid water created by roiling the bottom of a clear area with window screening (Station 4H).

Males of this species taken on the 21st of December from gravel riffles of the lower Arroyo Encino exhibited breeding tubercles, and spawning may have been in progress at the time of capture.

Stations: 1G, H, J–L; 2A; 3A–C; 4B, D–L; 6B–E; 8A, B.

Museum Nos.: CNHM 4477, 62644, 62654, 62674; TU 5573, 5579, 5589, 5595, 5605, 5609, 5615, 5627, 5648, 5683, 5688.

Dionda sp.

Known only from the Río Tamesí.

In the present study 197 specimens of this undescribed minnow were taken from the headwaters of the Río Tamesí. The species appeared in collections from the lower two-thirds of the Río Sabinas, the Nacimiento of the Río Frío, the Río Mante and the Río Guayalejo at Adjuntas. This fish is primarily an inhabitant of clear waters which show a fair current, and to some extent it replaces *D. rasconis* in such habitats. The two species were frequently taken together, however. This minnow was seldom taken in large numbers except in the clear, slow, weedy waters of the Río Frío near its Nacimiento. In the clear flowing irrigation ditch of the Río Mante this species was easily recognized, and large numbers were observed together with *A. fasciatus* and *G. vittata* feeding upon the filamentous algae and other organic matter which could be gleaned from the surface of a concrete culvert. Because of the depth and current the seine collection (7A) does not fairly represent the abundance of *Dionda sp.* at this location. This handsome minnow is notable in possessing a dark, well-defined, unbroken lateral band characteristic of certain fishes which inhabit clear flowing streams. The association of this minnow with *Gambusia vittata* is discussed later.

Males of this minnow taken on the 21st of December from gravel riffles of the lower Arroyo Encino exhibited well-developed breeding tubercles, and spawning may have been in progress at the time of capture. Although both species of *Dionda* apparently spawn in riffles at about the same time, field data suggest that the breeding aggregations tend to occupy slightly different habitats, either different riffles or different areas of the same riffles.

Stations: 1J–L; 4D–F, K, L; 5A; 7A, D; 8B.

Museum Nos.: CNHM 62653, 62665, 62673; TU 5571, 5580, 5649, 5668, 5678.

Notropis lutrensis (Baird and Girard). Red shiner

Nototropis forlonensis Meek. Meek (1904, Valles, Forlón)

Cyprinella forlonensis (Meek). Jordan, Evermann, and Clark (1930)

Notropis lutrensis forlonensis Meek. Hubbs (1954)

Originally distributed from South Dakota, Minnesota, and Illinois southward and and westward through Texas into northern Mexico; in Gulf coastal streams as far south as the Río Pánuco system.

In the present study 70 specimens were obtained from the lower two-thirds of the Río Sabinas and from the Río Guayalejo at Adjuntas. It was not encountered in the Ríos Frío, Boquilla, or Mante or in the Laguna de Chairel. In the Río Sabinas this minnow was taken only in the deeper pool areas with or without current. It appears to be primarily an inhabitant of the larger downstream waters, and future collecting should reveal this species in larger waters of the Río Tamesí itself.

Examination of the stomach contents of five individuals revealed over 20 insects, one water mite, six large protozoa, and some filamentous algae and detritus. These minnows appeared to have been feeding rather selectively upon insects, and the algae and detritus were probably incidental.

Meek (1904) stated that the spawning time is the latter part of May. This was not verified by the specimens examined in the present study since the ovaries of all females appeared to be immature. Some of the males, however, appeared to be developing breeding tubercles which might suggest a late spring (June) spawning.

Stations: 4H,J–L; 8A,B.

Museum Nos.: CNHM 4478, 4479, 62656, 62676; TU 5654, 5682.

Notropis sp.

Known only from the Río Tamesí.

In the present study 144 specimens of this undescribed minnow were taken from the headwaters of the Río Tamesí. Specimens were obtained from the middle and lower stretches of the Río Sabinas and the Río Guayalejo at Adjuntas. It was not found in the Ríos Frío, Boquilla, or Mante or in the Laguna de Chairel. The distribution of this minnow appears to be somewhat similar to that of *N. lutrensis*. The abundance of the present species in the Río Guayalejo and in certain backwater areas around Storms' Ranch, however, suggests that, whereas this fish does inhabit the larger rivers, it is also at home in shallow upstream backwaters such as the mouth of the Arroyo Encino.

During the course of the field work numerous observations were recorded of small cyprinid fishes swimming in loose schools at the surface of deep (2–3 m) clear water in the Río Sabinas around Storms' Ranch. These minnows often nibbled at the organic material present on tree roots at the edge of the deep water and were immediately attracted to any minor surface disturbance, such as an insect falling into the water. The individuals would scatter at any major disturbance but would return shortly to continue their surface activity. Although the identification is not positive, these observations apparently relate to the present species. Specimens of this small surface minnow could be captured selectively by a small-meshed net lowered below the surface of the water and quickly raised after the fish had returned.

Stations: 1K, L: 4D, F, I, K, L; 8B.
Museum Nos.: CNHM 62655, 62675; TU 5572, 5578, 5655, 5681.

Ariidae—Sea Catfish Family

Galeichthys felis (Linnaeus). Sea catfish
Galeichthys güntheri Regan. Jordan and Dickerson (1908, Tampico)
Galeichthys felis (Linnaeus). Hubbs (1936)
Along Atlantic coast of North America from Cape Cod to Florida, and along Gulf coast at least as far south as Vera Cruz and Yucatán, Mexico.

The sea catfish is one of the most abundant species inhabiting the estuaries of the northern Gulf coast, and it has been reported from the mouths of tropical rivers some distance from the Gulf in southern and eastern Mexico by Hubbs (1936). Its presence in the Tampico lagoons is anticipated. Food habits of the sea catfish on the northern Gulf coast have been studied by Gunter (1945), Darnell (1958), and others, and the spawning season in southern Texas has been discussed by Gunter (1945, 1947).

Station: 9A.

Ictaluridae—Catfish Family

Ictalurus australis (Meek). "Bagre"
Amiurus australis Meek. Meek (1904, Forlón)
Ichthyaelurus punctatus (Rafinesque). Meek (1904)
Streams entering the Gulf in east-central Mexico from the Río Tamesí south to the Río Blanco in southern Vera Cruz.

This fish is a close relative of *I. punctatus,* but, according to Carl Hubbs (personal correspondence), it constitutes a distinct species.

In the present study 56 specimens of this catfish have been taken from the upper and middle stretches of the Río Sabinas, from the Boquilla and from the Guayalejo at Adjuntas. Young individuals were taken by seine in the muddy waters of the Río Boquilla and Río Guayalejo. Adults are not as readily taken by seine, particularly in the daytime. Observations as well as captures with hooks and fyke nets indicated that this species is abundant in the Río Sabinas as far up as the Nacimiento, and a single adult specimen was obtained from a rocky pond in the Arroyo La Flor above the Nacimiento. The species is undoubtedly of widespread distribution within the drainage in both clear and turbid waters of the tributaries and larger rivers, as well.

In the clear waters around Storms' Ranch *I. australis* was frequently observed, and the observations were verified by specimens. This catfish resides during the day in caves and crevices under the banks, especially where they are undercut by the current or where roots of cypress trees form extensive caverns under the banks. These shelters are shared during the daytime with the giant tropical freshwater shrimp, *Macrobrachium carcinus,* and they provide temporary haven for large cichlids, *C. cyanoguttatum,* when the latter are disturbed. The catfishes may be drawn out of the crevices and even captured on a hook in the daytime by the strong odor of decaying flesh (rotten beef liver is most effective). They normally remain hidden during the day, however, and become active at dusk. At first one or two will venture a short way from the shelter, swim around for a moment, then return. This procedure continues

with increasing numbers until the entire local school has become active. These then approach the center of the stream, form a column, and proceed roughly in single file down to the neighboring pool for night-time foraging. In such columns the largest individual is foremost, and subsequent individuals are ranked in approximate order of size with the smallest seemingly playing an irresponsible game of tag at the rear of the column. At night they are readily taken in the pools by trot lines, hand lines, or fyke nets.

Stomach contents of six individuals were examined, and all contained much food material. Two small specimens from the Río Boquilla had fed directly upon bottom material and contained much detritus and many insect larvae (mostly Diptera, but including some Ephemeroptera and Odonata). Larger individuals from the Río Sabinas had consumed a wide variety of food items of plant and animal origin. Plant material included fruit of the strangling fig tree (*Ficus segoviae*), and various seeds, buds, and bits of leaves. Animal material included aquatic insects, exoskeleton of the tropical river shrimp, *Macrobrachium carcinus*, and remains of cichlid fishes. Some detritus and undetermined organic matter were also present. Food habits of this species appear to be quite similar to those of the closely related channel catfish (Darnell, 1958).

Gonads of all specimens appeared to be immature in the spring.

Stations: 1N; 3C; 4D,E,G; 6B–D; 8A,B.

Museum Nos.: CNHM 4474, 4475, 62646, 62688; TU 5594, 5611, 5625, 5660, 5693.

Ictalurus furcatus (LeSueur). Blue catfish, "Bagre," "Pintontle"

Ictalurus furcatus (LeSueur). Jordan and Snyder (1901, Tampico), Jordan and Dickerson (1908, Tampico)

Ichthyaelurus furcatus (LeSueur). Meek (1904)

Principally in large rivers from the Mississippi River valley west and south to the Pánuco-Tamesí drainage.

This catfish, which has been recorded in the Río Tamesí system as *I. furcatus* and which is clearly a southern representative of this group, may be sufficiently divergent to warrant its eventual separation as a distinct species (Carl Hubbs, personal correspondence). In the present study 19 specimens were taken in two collections from deep pools in the Ríos Boquilla and Guayalejo. Although the blue catfish is not readily taken in small seines, its absence from upstream collections by various types of gear suggests that the species inhabits the larger, more turbid waters, and it is probably abundant in the Río Tamesí proper. This species may occasionally enter the headwaters, and a large catfish captured several years ago at Storms' Ranch which was said to have weighed about twenty-five pounds probably belonged to this species. The blue catfish may also be present in the deeper portions of the Ríos Mante and Frío, and since the species is known to be a frequent invader of brackish-water areas (Gunter, 1945; Darnell, 1958), it might be expected to occur in the lagoons around Tampico.

Food habits of the blue catfish on the northern Gulf coast have been discussed by Darnell (1958). In the present study the stomach contents of five small specimens from the Río Boquilla were examined. These contained a great many immature and adult insects (chiefly dipteran larvae, but also including Coleoptera, Ephemeroptera,

and Hymenoptera). Other material included eggs (probably fish roe), balls of algae, and bits of undetermined organic matter and detritus. Food of adult blue catfish in the Tamesí area has not been studied.

Stations: 6D, 8B, 9A.

Museum Nos.: CNHM 62645; TU 5659.

Ictalurus mexicanus (Meek).

Amiurus mexicanus Meek. Meek (1904, Rascón, Río Verde)

Ictalurus mexicanus (Meek). Miller (1956, Río Pánuco)

Known only from the Pánuco-Tamesí system.

This little catfish is closely related to *I. lupus* of the streams farther north, but according to Carl Hubbs (personal correspondence) the Pánuco-Tamesí form represents a distinct species. The material reported here represents the first record of its occurrence in the Río Tamesí. In the present study three specimens were obtained in a single collection from the Río Guayalejo at Adjuntas. The same collection contained specimens of both the other known species of the genus and permitted the first clear analysis of the *Ictalurus* complex from this drainage, establishing the validity and relationships of *I. mexicanus*. Since this species appeared only in the single collection, its intradrainage distribution is not understood.

I. lupus has been considered by Hubbs, Kuehne, and Ball (1953) and others to be an inhabitant of springs and other headwaters in the Texas streams. The same may be true of the southern representative, *I. mexicanus*, but at present there is no evidence to support this concept.

Station: 8B.

Museum No.: TU 5653.

SYNGNATHIDAE—Pipefish Family

Oostethus lineatus (Kaup). Opossum pipefish

Doryrhamphus lineatus (Valenciennes). Jordan and Dickerson (1908, Tampico lagoons)

Oostethus lineatus (Kaup). Hubbs (1929)

Both sides of the Atlantic and in the New World from South Carolina to Brazil; also found in Cuba and a number of the West Indian islands.

No pipefishes were taken during the present study. Herald (1942) pointed out that a number of nominal species are probably synonyms of *O. lineatus*, and he also modified the known geographic range of the species. Hubbs (1929) noted that this pipefish is chiefly an inhabitant of brackish waters, but that it ranges into purely fresh water and doubtless also into the sea. Hildebrand (1939), however, indicated that this fish is quite at home in the fresh waters of Panama, and he took males bearing eggs from Gatun Lake, showing that the fish breeds in the lake and that it is probably a permanent resident there.

Station: 9A.

CYPRINODONTIDAE—Killifish Family

Cyprinodon variegatus Lacépède. Sheepshead minnow

Cyprinodon elegans Baird and Girard. Jordan and Snyder (1901, lagoons near Tampico)

Coastal lagoons from Maine to South America and throughout the West Indies.

C. elegans is now considered to be restricted to certain localities in Texas (Miller, 1951), and *C. variegatus*, which is known to extend at least as far south as the tip of Yucatán (Miller, 1955), is the only representative of this genus whose presence in the lagoons around the mouth of the Río Tamesí would be anticipated. No specimens of any *Cyprinodon* were obtained in the Laguna de Chairel collections, and the presence of this estuarine species in the drainage needs verification.

Station: 9A.

Fundulus grandis Baird and Girard. Gulf killifish

Fundulus heteroclitus (Linnaeus). Jordan and Snyder (1901, lagoons near Tampico)

Fundulus grandis Baird and Girard. Miller (1955)

Brackish waters from northeastern Florida westward along the northern Gulf coast and south along the Mexican coast at least to Laguna de Tamiahua, south of Tampico; also on north coast of Cuba.

Miller (1955) has shown that *F. heteroclitus* is restricted on the Gulf coast to the state of Florida, and he has further indicated that *F. grandis* extends south along the Mexican coast past Tampico. Regarding its habitat, Miller (1955) has pointed out that the species is found typically in brackish water, less commonly entering full sea water, and penetrating fresh water in the southern part of its range. No specimens of the gulf killifish were obtained in the Laguna de Chairel collections, and the presence of this species in the drainage, although highly probable, is in need of verification.

Station: 9A.

Fundulus similis (Baird and Girard). Longnose killifish

Fundulus similis (Baird and Girard). Miller (1955, north of Tampico)

Brackish water from northeastern Florida along the northern Gulf coast and southward into Mexico at least as far as a lagoon 35 miles north of Tampico.

The longnose killifish has never been recorded from the Río Tamesí drainage, and it is listed here on the basis of Miller's (1955) record from a lagoon 35 miles north of Tampico. The species is known to enter nearly fresh water (Gunter, 1945, 1950; Reid, 1954), and, although it is anticipated, its presence in the drainage should be verified.

Lucania parva (Baird and Girard). Rainwater killifish

Lucania venusta Girard. Meek (1904, lagoons north of Tampico)

Coastal swamps of the eastern United States from Massachusetts south and west across the Gulf coast to Texas and New Mexico, then south to Tampico, Mexico.

Two specimens taken from the Laguna de Chairel in the present study represent the first record of this species from the Tamesí drainage. Since the rainwater killifish is known to enter fresh water in the southern part of its range, this species may be distributed rather widely in the low-lying coastal marshes of the Tamesí drainage area.

Station: 9B.

Museum No.: TU 5634.

POECILIIDAE—Livebearer Family

Gambusia affinis (Baird and Girard). Mosquitofish

Gambusia affinis (Baird and Girard). Jordan and Snyder (1901, Tampico lagoons), Meek (1904, Rascón, Valles, Forlón), Regan (1913, Tampico)

Originally native from Alabama and southern Illinois south and west through Texas and south along the Mexican coast to the Pánuco-Tamesí system.

Early workers did not distinguish between this and the several other gambusias which inhabit the drainage. Therefore, all records before Hubbs' (1926) study of the genus are doubtful. Hubbs (1926) reexamined Meek's specimens from Rascón, Valles, and Forlón, and from this material he described three new species, *G. panuco*, *G. regani*, and *G. vittata*. Hubbs (1926) made no mention, however, of *G. affinis* or of another (undescribed) species in the Pánuco-Tamesí complex. As pointed out by Bailey, *et al.* (1954), Gunter (1956), and others, *G. affinis* is a frequent invader of brackish water.

In the present study 107 specimens of *G. affinis* were obtained in collections from the Río Mante and from the Laguna de Chairel at Tampico. Its presence in these collections and its absence from others suggest that in the Tamesí area the species prefers lake-like conditions with ample vegetation and virtually no current. This species was never collected with either *G. panuco* or *G. regani*, which occupy somewhat similar habitats in the other tributaries. Each of the three species appears to have become better adapted than the other two to life in a particular headwater stream. The mutually exclusive distributions of these three very similar and closely related species suggest competitive elimination of ecologically equivalent species. *G. affinis* was taken together with *G. vittata* and *Gambusia sp.* As mentioned below the habits of *G. vittata* are quite different and, indeed, unusual for a gambusia, implying little competition with the other gambusias. Not enough is known about the habitat of the new species of *Gambusia* to comment on relations with its congeners.

Analysis of the stomach contents of three individuals revealed three adult insects, two water mites, and little else. Simpson and Gunter (1956) reported that two specimens from the coastal waters of Texas contained small fish, small crustaceans, and annelids. This gambusia is widely recognized as a voracious predator on small arthropods, consuming both aquatic forms and non-aquatic insects which fall to the surface of the water.

Krumholz (1948) has considered in detail the reproductive habits of this species in Illinois.

Stations: 7B–D; 8A (?); 9A (?), B.

Museum Nos.: CNHM 62666; TU 5637, 5673.

Gambusia panuco Hubbs.

Gambusia affinis (Baird and Girard). Meek (1904, Rascón, Valles) (in part)

Gambusia panuco Hubbs. Hubbs (1926)

Known only from the Pánuco-Tamesí drainage system.

In the present study 209 specimens were obtained in five collections from the Río Boquilla thereby extending the known range of the species to the Río Tamesí system. This gambusia which appeared to be widespread in the Boquilla was not encountered elsewhere in the drainage, nor was any other species of gambusia taken in the Río Boquilla, not even the wide-ranging and ecologically divergent *G. vittata* with which it apparently did occur in Meek's Valles collection. Within the Río Boquilla drainage *G. panuco* seemed to prefer the smaller, less turbid waters, but it was also fairly abundant in the deeper arroyo and the very turbid pools of the Río Boquilla proper. It was least frequent in the lake. On the basis of its wide habitat tolerances, this species

would certainly have been expected to occur in the Río Sabinas and, perhaps, in the Ríos Frío and Mante.

Unfortunately, the stomach contents of only two specimens were examined. Together these contained two insects, four water mites, one cladoceran, one rotifer, and numerous arthropod egg cases. This fish apparently subsists upon small arthropods and zooplankters. One large female collected in early April contained 17 well-developed young.

Stations: 6A–E.

Museum Nos: CNHM 62647; TU 5610, 5619, 5623, 5632.

Gambusia regani Hubbs.

Gambusia affinis (Baird and Girard). Meek (1904, Forlón) (in part)

Gambusia regani Hubbs. Hubbs (1926)

Known only from the headwaters of the Río Tamesí.

Hubbs (1926) suggested that *G. regani* probably also occurs in the Río Soto La Marina which enters the Gulf north of the Tamesí, but this has not been confirmed. In the present study 171 specimens were obtained from the Río Sabinas and its tributary arroyos, and a single questionable specimen appeared in the Río Guayalejo collection near the mouth of the Río Sabinas. *G. regani* is a fish of small pools and shallow, weedy backwaters, and it was seldom found in water with more than a very slight current. Its center of population density appeared to be the Arroyo Encino where it was taken in almost every arroyo seine collection from the springs above Encino down to the junction with the Río Sabinas. It also appeared in ponds above the Nacimiento and in backwaters throughout the length of the Río Sabinas. This fish was never found in large concentrations.

Stomach contents of 20 specimens were examined of which 18 contained food. Larval and adult insects made up 85 per cent of this material. About half of these insects were chironomid larvae, but the larvae of Coleoptera and Trichoptera and adults of Coleoptera, Diptera, and Hymenoptera also were present. Additional animal remains included a well-digested snail, a water mite, and arthropod eggs. A few strands of filamentous algae and a small amount of detritus made up the remainder. Over 95 per cent of the material encountered was of animal origin, and it is clear that this highly predaceous little fish subsists almost entirely upon small arthropods with emphasis upon chironomid larvae.

Seven females taken in late April and early May all contained young. Six females 23–27 mm in length averaged 5.8 embryos per female, whereas the single large female (32 mm) contained 13 mature young.

Stations: 1B–E,G,H,J–L; 2A; 3C,D; 4A,B,F,G,J–L; 8B (?).

Museum Nos.: CNHM 14033–45, 62657, 62678; TU 5568, 5575, 5588, 5596, 5658(?), 5679.

Gambusia vittata Hubbs.

Gambusia affinis (Baird and Girard). Meek (1904, Valles) (in part)

Gambusia vittata Hubbs. Hubbs (1926)

Known only from the Pánuco-Tamesí drainage system.

In the present study 1,139 specimens were taken from the headwaters of the Río Tamesí. This gambusia was obtained from the middle and lower stretches of the Río Sabinas, the Ríos Frío and Mante, and the Río Guayalejo at Adjuntas. The distribu-

tion of this fish closely parallels that of *Dionda sp.* Both species were absent from the Arroyo Encino except near the Río Sabinas. Both were absent from collections made in pools of the Arroyo La Flor, the Nacimiento, and upper reaches of the Río Sabinas, the Río Boquilla, and the Laguna de Chairel. Unlike *Dionda sp.*, however, *G. vittata* was generally present in large numbers in suitable environments of the Río Sabinas, and the habitat relations of this species can be stated with greater certainty. This gambusia inhabits clear waters with slow to moderate current. It was often abundant in weedy backwaters and areas of dense algal growth. In the Sabinas and lower pools of the Arroyo Encino this species was often present with *G. regani*, but the two species were never abundant together. In the Río Mante *G. vittata* was present in several collections with *G. affinis*, and these two were obtained together with *Gambusia sp.* in a single collection. *G. vittata* was not present in the Río Boquilla with *G. panuco*, but they both apparently occurred together in Meek's collection from the Río Pánuco (Valles). From the available evidence it appears that *G. vittata* is not an important ecological competitor with any of the other species of *Gambusia*. It tends to inhabit clearer and swifter waters than any of the other species, and, as pointed out below, its food habits are remarkable for a member of this genus. This gambusia parallels *Dionda sp.* in the possession of a dark, well-defined, unbroken lateral band.

Stomach contents of 20 specimens were examined, of which eighteen contained food. Fifty per cent of the material encountered was filamentous algae (mostly *Spirogyra* with some *Rhizoclonium*). This fish exhibits the unusual ability to swallow *Spirogyra* in neat sheaves with the strands parallel, rather than in balls or tangled networks as a number of other small fishes do. Arthropods made up only 20 per cent of the stomach contents and included the remains of insects, water mites, and arthropod eggs. Protozoa (*Arcella*) constituted one per cent, and undetermined organic matter and detritus made up the remainder. The habit of consuming large amounts of algae and detritus is not at all typical for fishes of the genus *Gambusia*, and they seem to be primitive characters rather than recent specializations within the genus. If these stomach contents are truly representative, this fish does not closely compete for food with any other gambusiin fish examined. As mentioned below an interesting relation apparently exists between feeding habits and reproductive habits.

Of the nine females examined from April collections, only one failed to contain developing young. Females 25–30 mm averaged 9.5 young per pregnant female, whereas the single 31 mm female possessed 14 developing embryos. In most collections the sex ratio was about even, but one backwater collection (4D) contained 45 females and a single male and appeared to have taken females "in labor." This collection was made in water a few centimeters in depth with many *Spirogyra* mats floating on the surface and clinging to the rocks. Three females with mature eggs had eaten well. Three females with large young (including one which had apparently already delivered several young) had fed very little. One female which had obviously recently delivered her brood was stuffed with food. All females with mature young and the recently delivered female had consumed only algae, but the others also included arthropods. If the situation is interpreted correctly, it appears that this fish, which normally remains close to the current, enters the very shallow, algae-laden backwaters largely for delivery of the young. As the young near full term the female undergoes a period of fasting. After the young are born the female feeds heavily,

but, to avoid the danger of consuming her own young, she becomes largely a vegetarian during this period. For this reason the algae-eating habits of this species may be somewhat exaggerated, but it is quite remarkable that they consume algae at all.

Stations: 1J–L; 4D–F, H–L; 5A; 7A–D; 8A,B.

Museum Nos.: CNHM 14046–58, 62658, 62668, 62677; TU 5570, 5576, 5656, 5665, 5671, 5676.

Gambusia sp.

Known only from the Río Tamesí drainage.

Seven specimens of this undescribed species of *Gambusia* were obtained in a single collection from the reservoir of the Río Mante. Judging from its occurrence in the reservoir collection this species probably inhabits weedy margins of lake-like areas. Nothing is known regarding its food or breeding habits. According to Hubbs (personal correspondence) this is not the species which Ahl (1923) described from "habitat Mexico" as *G. modesta* and later (1925) changed to *G. myersi* because of preoccupation of the former name.

Station: 7D.

Museum No.: CNHM 62667.

Mollienesia formosa (Girard). Amazon molly

Mollienisia formosa (Girard). Regan (1913, Tampico) (incorrectly), Hubbs and Hubbs (1932)

Streams from southwestern Texas south to the Río Tamesí.

C. L. Hubbs (1926) suggested that Regan's material listed as *M. formosa* probably included specimens of *M. latipinna* and *M. sphenops* which were previously known from the drainage, and in 1933 Hubbs pointed out that this material was actually referable to *M. latipinna*. In 1932 C. L. Hubbs and L. C. Hubbs recorded live specimens which had been taken from Forlón in the Tamesí drainage for breeding purposes. In the present study a single specimen of the Amazon molly was collected from the Río Guayalejo at Adjuntas in the company of *M. sphenops*. Bailey and Miller (1950) have discussed the spelling of the generic name.

Habitat relations and food habits of this species have not been studied within the drainage. Judging by its close association with the euryhaline *M. latipinna*, at least in the Texas portion of its range, this fish probably enters waters of low salinity, but confirmatory records seem to be lacking.

The remarkable sexual condition and reproductive behavior of this species based upon extensive laboratory breeding experiments have been considered in a series of papers by C. L. Hubbs (1933, 1934, 1955) and by C. L. Hubbs and L. C. Hubbs (1932, 1946). Meyer (1938) studied cytogenetic aspects of reproduction in the Amazon molly. Recently Clark Hubbs, Drewry, and Warburton (1959) described a single male specimen from southern Texas which they interpreted as being a male representative of *M. formosa*. Miller and Schultz (1959), however, have pointed out that the specimen might have been a hybrid between *M. sphenops* and *M. latipinna*. The latter authors also reported the all-female but non-gynogenetic condition in a related group of poeciliid fishes (*Poeciliopsis*) from northwestern Mexico.

As noted by Hubbs and Hubbs (1932), in the headwaters of the Río Tamesí *M. sphenops* is undoubtedly the species with which *M. formosa* consorts. If the Amazon molly does frequent the coastal lagoons around Tampico, it probably enjoys intimate

association with males of both *M. sphenops* and *M. latipinna. M. latipunctata,* which is more distantly related, undoubtedly does not become involved.

Station: 8A,B.

Museum Nos.: CNHM 15592–16647; TU 5651.

Mollienesia latipinna LeSueur. Sailfin molly

Mollienisia latipinna LeSueur. Jordan and Snyder (1901, Tampico lagoons), Regan (1908, Tampico), Hubbs (1926, 1933)

Mollienisia formosa (Girard). Regan (1913)

Coastal swamps from South Carolina across the northern Gulf and south along the Mexican coast to Campeche.

As mentioned previously, Hubbs (1926, 1933) pointed out that specimens which Regan (1913) recorded from Tampico as *M. formosa* were, in reality, *M. latipinna.* The sailfin molly was not taken in the present study, not even in the large collection from the Laguna de Chairel. The species is known to enter freshwater, however, and further collecting will be necessary to establish details of its distribution in the lagoons about Tampico.

Ecological relations of the sailfin molly on the Texas coast have been discussed by Gunter (1945, 1950) and by Simpson and Gunter (1956).

Station: 9A.

Mollienesia latipunctata (Meek).

Poecilia latipunctata Meek. Meek (1904, Forlón)

Mollienisia latipunctata (Meek). Hubbs (1933)

Known only from the headwaters of the Río Tamesí.

Hubbs (1933) pointed out that this species is limited to the Río Tamesí and its tributaries. In the present study 464 specimens were taken from the waters of the Río Mante, although the species did not appear in any of the other collections from the drainage. This molly was well represented in all of the Río Mante collections, but it was particularly abundant in the collection made at the Nacimiento (7C) where the water was deep, clear and flowing and contained extensive beds of submerged vegetation. Since the Río Mante collections covered a wide range of habitat types, the absence of this fish from collections in the other tributaries may have been due to biological rather than to physical factors. *M. sphenops* which was widely distributed throughout the headwaters of the Río Tamesí was present with *M. latipunctata* in all of the Río Mante collections. In the irrigation ditch and reservoir where *M. latipuctata* was abundant *M. sphenops* made up less than five per cent of the collections. Below the dam, however, where creek-like conditions prevailed, *M. sphenops* was more than twice as abundant as *M. latipunctata.* The spotted molly appears to be more at home in deep, clear waters, but future work will be required to clarify the observed distribution patterns. It should be pointed out that the lateral spots on *M. latipunctata,* particularly the females, form a dark, almost continuous lateral band effect somewhat similar to that observed in *D. rasconis* and *G. vittata,* which also tend to inhabit clear flowing waters.

Stomach analyses were carried out on five specimens. These all contained much mud and bottom ooze with which were mixed a few strands of green and blue green algae and some diatoms and sand grains. This species obviously feeds from the bottom, but the location, mechanics, and behavior of feeding are unknown.

Meek (1904) mentioned that a specimen taken at Forlón in mid-May contained 16 developing young. In the present study four females collected in early June were found to possess immature eggs, and at least one group had been fertilized. Hubbs (1933) indicated that in laboratory aquaria this species produces very small broods, and although the young are large at birth they develop very very slowly.

Stations: 7A–D, 8A.

Museum Nos.: CNHM 4484, 4485, 62669; TU 5672.

Mollienesia sphenops (Valenciennes).

Poecilia limantouri Jordan and Snyder. Jordan and Snyder (1901, Río Tamesí, Tampico, Rascón, Río Verde)

Poecilia sphenops Cuvier and Valenciennes. Meek (1904, Forlón)

Mollienisia sphenops (Cuvier and Valenciennes). Regan (1913), Hubbs (1933)

Coastal streams from the Río Grande basin southward to northern South America.

In the present study 2,949 specimens were taken from most collections made in the Ríos Sabinas, Frío, Boquilla, Mante, and Guayalejo. Although the species failed to appear in the Laguna de Chairel collection, the reference by Jordan and Snyder (*loc. cit.*) confirms its presence in the low coastal lagoons. This fish is known to enter brackish-water, and Gunter (1956) has considered it to be euryhaline. This molly is distributed widely throughout the shallow waters of both the Pánuco and the Tamesí, and, in the latter stream at least, it is one of the three most abundant species (together with *A. fasciatus* and *D. rasconis*).

This molly is a bottom inhabitant, and although it has wide habitat tolerances it seems to prefer small creeks where it utilizes both shallow pools and riffles. This fish shows a decided preference for rocky bottoms which are richly covered with a carpet of ooze containing some filamentous algae (especially blue-greens), diatoms, protozoans, and decaying bits of leaves and other matter.

Silt bottoms also are accepted, and, as indicated by its presence in the Río Boquilla collections, the species exhibits a wide tolerance for turbidity. This molly was most often found in circumstances where the current was slow or absent, and it was generally not abundant in larger bodies of water or where the current was moderate to swift. During the spring, however, when torrential rains send rivers over their banks and connect roadside ditches with the creeks and arroyos, swarms of these adventurous little fish swim upstream and are seen to be active in small surface waters everywhere throughout the countryside several miles from the nearest permanent water. Comparative habitat relations and possible ecological competition between this species and *M. latipunctata* have already been mentioned.

Stomach analyses were carried out on eighteen specimens, of which seventeen contained food. Each stomach possessed much unidentifiable detritus and decaying organic matter, as well as filamentous algae (*Lyngbya, Oscillatoria, Spirogyra, Ulothrix, Uronema*), diatoms (*Navicula, Pinnularia, Sirurella*), desmids (*Cosmarium, Pediastrum*), and bits of vascular plant material. Some silt and sand also were encountered. Even though the fishes for stomach analyses were purposely selected from several different stations and environments, the stomach contents varied only slightly from one individual to another. This molly feeds from the exposed surfaces of rocks, stones, and other bottom features. It apparently utilizes its broad, flat, tooth-covered lower lip as a brush or rasp to clean the algae and other accumulated living and non-

living matter from such surfaces. Whereas little sorting of the rasped food seems to be involved, the fish obviously exhibits selectivity in determining the surfaces to be used for feeding.

All eight of the females examined above forty mm in length which had been taken in April contained developing young. The number of young varied with the size of the female from 13 in the smallest to 35 in the largest, and one of the larger females contained 52 mature but unfertilized eggs. Brood sizes in aquarium-reared *M. formosa*, *M. latipinna*, and *M. sphenops* were given by Meyer (1938), who found the maximum number per female to be 105, 84, and 117, respectively. Krumholz (1948), however, reported a female *Gambusia affinis* with 315 developing embryos.

As mentioned earlier *M. sphenops* is one of the species which normally inseminates the females of *M. formosa*, and it is probably the primary species involved in such activity throughout most of the Río Tamesí drainage where *M. formosa* is found. Possible hybridization between *M. sphenops* and *M. latipinna* has been noted in the Tampico area by Hubbs (1933), but *M. sphenops* probably does not hybridize with *M. latipunctata* in nature.

Stations: 1B–H,J–L; 2A; 3A–D; 4A–G,J–L; 5A; 6A–E; 7A–D; 8A,B; 9A.

Museum Nos.: CNHM 4483, 62648, 62659, 62670, 62679; TU 5567, 5582, 5584, 5592, 5602, 5604, 5613, 5618, 5620, 5630, 5650, 5664, 5669, 5680, 5687.

Xiphophorus montezumae Jordan and Snyder. Montezuma swordtail

Xiphophorus montezumae Jordan and Snyder. Jordan and Snyder (1901, Río Verde, near Rascón)

Known only from the Pánuco-Tamesí drainage system.

In the present study 85 specimens were obtained from the headwaters of the Río Sabinas and of the Río Frío. Downstream collections failed to yield specimens. In the Río Sabinas a small population of swordtails was encountered in the long side pool at the Nacimiento, and occasional individuals appeared in collections from ponds in the Arroyo La Flor above the Nacimiento and in a single backwater collection from the Sabinas above Storms' Ranch. In the headwaters of the Río Tamesí this species lives in clear weedy waters, especially in the vicinity of springs, and appears to have very narrow habitat tolerances.

Comparative habitat relations of this species and *X. variatus* are discussed in the next section. It might be mentioned here, however, that certain individuals of the Río Sabinas population of *X. montezumae* approach *X. variatus* closely in phenotype. Studies by Gordon (1947) have demonstrated the genetic basis of tail spotting in *X. maculatus* from the Río Papaloapan in Vera Cruz. Similar tail spots appear in the closely related *X. variatus* of the Río Tamesí. Certain swordtails of the Río Sabinas exhibit tail spotting similar to that of *X. variatus*, although in the swordtails the characters are much more weakly developed. This is an unusual characteristic among swordtails and is suggestive of past hybridization and introgression of *X. variatus* genes into the *X. montezumae* population. A genetic analysis should be carried out, especially in light of the following statement by Gordon (1953) who was familiar with the habitats of the species in the Río Pánuco:

"The ecological isolation of these species evidently explains why not a single wild hybrid between any of them has been discovered, although thousands of specimens have been collected and critically studied. This takes on added significance when it

is realized that under laboratory conditions, when their choice of mating partners is restricted, they are capable of producing hybrids of every possible combination."

Meek (1904) mentioned that females taken in May had developing eggs and that one 44 mm female contained 16 eggs.

Stations: 3C,D; 4A,B,E; 5A.

Museum Nos.: CNHM 62660, 62680; TU 5600, 5663.

Xiphophorus variatus (Meek). Variable platyfish

Platypoecilus variatus Meek. Meek (1904, Forlón)

Xiphophorus variatus (Meek). Gordon (1953, Rio Axtla)

Known only from the Pánuco-Tamesí system.

In the present study 173 specimens were obtained from the full length of the Arroyo Encino, several downstream areas of the Río Sabinas, the Río Frío near its Nacimiento, and two stations from the Río Boquilla. No specimens appeared in collections made from the Río Mante, the Río Guayalejo at Adjuntas, or from the Laguna de Chairel at Tampico.

This little platyfish was never abundant in any of the collections. The distributional pattern, however, reveals that it prefers quiet, shallow vegetated backwaters, and in the Río Sabinas it was taken only in backwater areas around beds of the pondweed, *Potamogeton illinoensis*. In the Arroyo Encino it was generally found around aquatic vegetation or in areas where many exogenous leaves and branches were present in the water. This platyfish was taken from very turbid water in the Río Boquilla, and it was the only species inhabiting the spring above Encino (1A) when the water was low in oxygen (3.2 ppm) and high in carbon dioxide (28.0 ppm). As indicated by Willmer (1934) and others, this is an unfavorable combination for many fishes.

Gordon (1953) has pointed out that in the Río Pánuco drainage *X. variatus* is usually found alone in the lowland areas, whereas in the uplands *X. montezumae* is taken exclusively in deep pools within the main channel of the river. In the intermediate areas a few individuals of both species may be found in shallow, sluggish backwaters and overflow pools. This is a fairly accurate description of the observed patterns of distribution in the Tamesí also, but, in the Río Sabinas at least, physiographic stream maturation occurs within a short distance so that apparently optimal habitat conditions for the two species occur within a few kilometers of each other. In the Río Frío the habitats may be closer or even contiguous, accounting for the fact that the two species were taken together from the Frío in some numbers. This foreshortening of the physiographic maturation in the headwater streams of the Tamesí and compression of habitats may also have resulted in introgressive hybridization as discussed in connection with the previous species.

Mollienesia sphenops, a related poeciliid, was frequently taken in collections with *X. variatus*. Observations revealed that, although the two species often occupy the same general habitats, the platyfish tends to remain in the shallow weedy peripheral areas, whereas the molly frequents bottoms in slightly deeper waters and is more intimately associated with rocks than with vegetation.

Analysis of the digestive tracts of eleven specimens revealed little variability in food habits. In all specimens unidentifiable mud or bottom ooze made up almost the entire bulk of the food, but traces of diatoms, desmids, filamentous green algae, and protozoa (*Arcella, Difflugia*) were often encountered. Feeding apparently takes place

during the day since specimens taken at 10:00 p.m. contained food only in the posterior half of the digestive tract. Most of the females examined from the spring collections possessed immature eggs, but one female taken May 8th carried eleven well developed young.

Stations: 1A,B,C,E,G,H,J,K,L,M; 2A; 3C; 4E,K,L; 5A; 6A,D; 8A.

Museum Nos.: CNHM 4486, 62649, 62661, 62681; TU 5581, 5587, 5601, 5631, 5662, 5684.

Mugilidae—Mullet Family

Agonostomus monticola (Bancroft). Mountain mullet

Florida, Louisiana, Mexican coast from the Río Tamesí south through Central America, and in Cuba, Puerto Rico and throughout West Indian islands; also known from Pacific coast.

The mountain mullet has not previously been reported from the Río Tamesí drainage, but from the known wide geographic distribution of the species in streams entering the Gulf of Mexico (Suttkus, 1956; Anderson, 1957b) its presence in suitable habitats would be anticipated. No specimens were taken in the present study, and the species is listed on the basis of numerous sight records throughout the upper reaches of the Río Sabinas. Specific sightings occurred in a pond of the Arroyo La Flor, in the Nacimiento and adjacent portions of the Río Sabinas, La Union, and several localities near Storms' Ranch. All efforts to capture this elusive fish proved futile, and a single dried and mutilated specimen brought in by one of the natives clearly belonged to the family Mugilidae but could not be distinguished further. Another mugilid which ascends streams of eastern Mexico is *Joturus pichardi* Poey, and some of the fast-swimming fishes seen in and around the Nacimiento of the Río Sabinas may eventually turn out to be this species.

In the Río Sabinas, as elsewhere (Evermann and Marsh, 1900; Hildebrand, 1938; Anderson, 1957b), the mountain mullet seeks out areas of clear, fast-flowing water of rocky streams, and in the Sabinas it was the only fish species which consistently inhabited the rapids and riffle areas (although a cichlid utilized them). It is a powerful swimmer, and even though individuals or small groups were easily approached within a few feet, various types of gear (including a shotgun) failed to procure specimens. Hildebrand (1938) mentioned that in Panamá this mullet feeds on small organisms such as insect larvae, sponges, and, apparently, algae.

Stations: 3A; 4A,B,D,E,G.

Mugil cephalus Linnaeus. Striped mullet, "Lisa"

Mugil cephalus Linnaeus. Jordan and Dickerson (1908, Tampico)

Widespread throughout tropical and subtropical shores of the world (known from all continents and many oceanic islands); along the east coast of the Americas from Nova Scotia to Brazil and throughout the West Indies.

In the present study during seining operations in the Laguna de Chairel the writer observed many striped mullets as they erupted from the marshes (seemingly from marginal areas above the water line) and as they leaped over the cork line of the seine. Only a single large specimen was taken. The striped mullet is known to ascend tropical streams for considerable distances above the influence of salt water. When

shown the specimen from Tampico, the natives of Storms' Ranch quickly agreed that this fish is not infrequently seen in the headwaters of the Río Sabinas where it is called "Lisa."

The striped mullet is primarily an iliophage, although quantities of algae frequently enter the diet. Food habits of the species on the northern Gulf coast have recently been discussed by Darnell (1958). Spawning habits of this fish in Florida have been noted by Breder (1940) and others.

Stations: 9A,B.

Museum No.: TU 5639.

Mugil curema Valenciennes. White mullet

Mugil curema Cuvier and Valenciennes. Jordan and Dickerson (1908, lagoon at Tampico)

Both sides of the Atlantic and along the American coast from Massachusetts to Brazil and throughout the West Indies; also known from the Pacific coast.

In the present study a single small individual appeared in the collection from the Laguna de Chairel. This widespread coastal species is known to enter fresh waters (Gunter, 1956). Food habits of the white mullet have not been studied in the area, but Ebeling (1957) has indicated that the species consumes diatoms and algal filaments. Anderson (1957a) discussed spawning of this species in the Atlantic Ocean off the east coast of Florida, and larval stages have been reported from the western Gulf off the Mexican coast in May by Caldwell and Anderson (1959).

Stations: 9A,B.

Museum No.: TU 5636.

CARANGIDAE—Jack Family

Caranx hippos (Linnaeus). Crevalle jack

Caranx hippos (Linnaeus). Jordan and Dickerson (1908, Tampico)

Warm and tropical seas of the world; along Atlantic coast from Nova Scotia south to Uruguay; also in the West Indies.

Although this species frequently enters bays, it is not often taken in shore seines. At the boat dock on the Laguna de Chairel the present writer observed a number of carangids which had been taken by sport fishermen. Hence, it is possible that both this and the following species are not uncommon in the lagoons about Tampico even though they have not appeared frequently in collections. The crevalle jack is a predator upon small fishes and invertebrates.

Station: 9A.

Caranx latus Agassiz. Horse-eye jack

Widely distributed throughout tropical seas of the world; along Atlantic coast of Americas from New Jersey to Brazil and throughout the West Indies.

Six small specimens of the horse-eye jack were taken in the present study from the Laguna de Chairel at Tampico. This is a common marine species throughout much of the Gulf, and even though it has been considered by Gunter (1942, 1956) to be euryhaline, it is seldom taken in waters of low salinity. The jackfishes are known to

be highly predaceous upon other fishes (Darnell, 1958), but the prey species in the Tampico lagoons are yet to be determined.

Station: 9B.

Museum No.: TU 5638.

LUTJANIDAE—Snapper Family

Lutjanus cyanopterus (Cuvier). Cubera snapper

Lutianus cyanopterus (Cuvier and Valenciennes). Jordan and Dickerson (1908, Tampico)

Atlantic coast of tropical America from Southern Florida south to Brazil; also present in Cuba and throughout the West Indies.

No specimens of this tropical marine snapper have been taken in the present study.

Station: 9A.

Lutjanus griseus (Linnaeus). Gray snapper

Lutianus griseus (Linnaeus). Jordan and Dickerson (1908, Tampico)

Both sides of the Atlantic and from Massachusetts south to Brazil; also found in Cuba, the Bahamas, and throughout the West Indies.

Hildebrand (1955) has indicated that the species is common thorughout the western Gulf and that a commercial fishery for this snapper exists on the Mexican coast as far north at Punta Piedras, Tamaulipas in Laguna Madre above Tampico. This fish is the only snapper which regularly enters the Texas bays (Gunter, 1945). The young inhabit shallow waters, but the adults may be encountered in shallow or deeper waters (Evermann and Marsh, 1900), and some preference has been noted for grassy areas (Reid, 1954). The gray snapper is euryhaline. It has been taken from waters of marine salinity and has been found to ascend streams of the Atlantic coast (Hubbs, 1936; Gunter, 1942). Behavior, color discrimination, and food habits of this interesting fish have been discussed by Longley and Hildebrand (1941). It is a predator upon invertebrates.

Station: 9A.

SPARIDAE—Porgy Family

Archosargus probatocephalus (Walbaum). Sheepshead

Archosargus probatocephalus (Walbaum). Jordan and Dickerson (1908, Tampico)

Archosargus oviceps Ginsburg. Ginsburg (1952)

Atlantic coast of North America from Cape Cod south at least as far as Yucatán, Mexico.

Ginsburg (1952) divided the sheepsheads of the Gulf coast into two species, and he included specimens from Tampico in the newly described form. H. Hildebrand (1955), however, pointed out that the new species, *A. oviceps* Ginsburg, is probably invalid. Hildebrand (1955) has further noted that this sheepshead is a frequent visitor in bays and estuaries along the northern Gulf coast and that it is caught commercially in large numbers in the bays of southern Texas and northern Mexico from Corpus Christi south to Tamiahua, Vera Cruz. The species has been recorded from fresh water (Gunter, 1942). Food habits of the sheepshead on the northern Gulf coast have been summarized by Darnell (1958). Smith (1907) and Hildebrand and Cable

(1938) discussed breeding habits of the species in North Carolina where it apparently spawns in the spring.

Station: 9A.

GERRIDAE—Mojarra Family

Numerous workers have pointed to the need for a critical revision of the family Gerridae (see, for example, Parr, 1927). This task has been partially accomplished by H. W. Curran (1942) in his Ph.D. thesis which, unfortunately, is still unpublished. This important study embodies a systematic revision of the genus *Eucinostomus,* and its relatives which are found in American waters. Generic designations given below follow those of Curran, although no attempt will be made here to justify their use.

Eugerres brasilianus (Cuvier).

Gerres plumieri Cuvier and Valenciennes. Jordan and Dickerson (1908, Tampico) (in part)

Diapterus brasilianus (Cuvier and Valenciennes). Meek and Hildebrand (1925)

Atlantic coast of tropical America from South Carolina to Brazil; also in Cuba and West Indian islands.

See statement under following species.

Station: 9A.

Eugerres plumieri (Cuvier). Striped mojarra

Gerres plumieri Cuvier and Valenciennes. Jordan and Dickerson (1908, Tampico) (in part)

Diapterus plumieri (Cuvier and Valenciennes). Meek and Hildebrand (1925)

Atlantic coast of tropical America from Florida and northern Mexico (Tampico) south to Brazil; also reported from Cuba and throughout the West Indies.

Meek and Hildebrand (1925) pointed out that Jordan and Dickerson's collection actually contained two species which they called *Diapterus plumieri* and *Diapterus brasilianus* (Cuvier and Valenciennes). Gunter (1942) reported that this species is probably euryhaline.

Station: 9A.

Eucinostomus melanopterus (Bleeker). Flagfin mojarra

Eucinostomus pseudogula (Poey). Jordan and Dickerson (1908, lagoons at Tampico)

Eucinostomus californiensis (Gill). Meek and Hildebrand (1925)

Eucinostomus melanopterus (Bleeker). Curran (1942)

From Louisiana and Texas south to Brazil; present in Cuba and West Indies; also found in Cape Verde Islands and along the Atlantic coast of tropical Africa.

Curran (1942) noted the errors of previous workers, and after examination of the Tampico material, he concluded that the specimens are referable to the tropical Atlantic species, *E. melanopterus*, originally described from Africa by Bleeker.

In the present study twelve specimens of this species were taken from the Laguna de Chairel at Tampico. As pointed out by Curran (1942) this gerrid ranges into brackish and fresh water.

Stations: 9A, B.

Museum No.: TU 5633.

SCIAENIDAE—Drum Family

Bairdiella ronchus (Cuvier). Ronco, Ground drummer

Bairdiella ronchus (Cuvier and Valenciennes). Jordan and Dickerson (1908, Tampico)

Atlantic coast of tropical America from northern Mexico (Tampico) south to Brazil; found in Cuba, and common throughout the West Indies.

This northernmost record for the species is in need of verification, especially in view of the fact that the northern representative of this genus, *B. chrysura*, is a common species in the bays of southern Texas (Gunter, 1945) and may penetrate southward as far as Tampico.

Station: 9A.

Gynoscion nebulosus (Cuvier). Spotted seatrout, speckled trout

Cynoscion nebulosus (Cuvier and Valenciennes). Jordan and Dickerson (1908, Tampico)

Both sides of the Atlantic and North America from New York south, at least as far as Tampico, Mexico.

Gunter (1952) noted that a fishery for this species exists in the Laguna Madre of the Mexican coast north of Tampico. In the estuaries of the northern Gulf coast where the spotted seatrout is quite abundant, it is primarily associated with quiet, clear lagoons and grassy flats, although it is sometimes encountered in turbid waters devoid of vegetation (Gunter, 1945; Moody, 1950; Reid, 1954, 1955; Darnell, 1958; Guest and Gunter, 1958). Food habits of this predatory species have been summarized by Moody (1950), Darnell (1958), and Guest and Gunter (1958). Spawning habits of the spotted seatrout has been discussed by Guest and Gunter (1958).

Station: 9A.

Micropogon undulatus (Linnaeus). Atlantic croaker

Micropogon undulatus (Linnaeus). Jordan and Dickerson (1908, Río Pánuco)

Along Atlantic coast of North America from Cape Cod south, at least as far as Yucatán.

Jordan and Dickerson (1908) reported taking "many dozens of immature specimens near the mouth of the Río Pánuco" which they called *Micropogon undulatus* (Linnaeus). Whereas this is the most likely species of croaker to be found in the area, it is possible that *M. furnieri* (Desmarest) also occurs as far north as southern Texas (see Hoese, 1958), and the ranges of the two species may overlap on the Mexican east coast. As indicated by Gunter (1945), Reid (1954, 1955, 1957), Darnell (1958), and others, the Atlantic croaker is one of the most abundant species of fishes inhabiting the muddy estuaries of the northern Gulf coast. The food habits of this fish have been discussed in detail by Darnell (1958). Pearson (1929) reported that the Atlantic croaker spawns from October to February in the Gulf of Mexico along the Texas coast.

Station: 9A.

Pogonias cromis (Linnaeus). Black drum

Pogonias cromis (Linnaeus). Jordan and Dickerson (1908, Tampico)

Bays and estuaries on the Atlantic coast of the Americas from Massachusetts south to Argentina.

This species is a frequent visitor in estuaries of the northern Gulf coast (Pearson,

1929; Darnell, 1958). It is relatively abundant in the waters of southern Texas (Hoese, 1958), and Gunter (1952) pointed out that this fish is taken commercially in some abundance from the Laguna Madre on the Mexican coast north of Tampico. The diet of the black drum consists primarily of mollusks, with a smaller percentage of crustaceans (Darnell, 1958). Pearson (1929) reported that this sciaenid spawns in Texas mainly from February to May.

Station: 9A.

EPHIPPIDAE—Spadefish Family

Chaetodipterus faber (Broussonet). Atlantic spadefish

Chaetodipterus faber (Broussonet). Jordan and Dickerson (1908, Tampico)

Along the Atlantic coast of the Americas from Massachusetts to Brazil.

As pointed out by Hoese (1958) this species is common in the shallow Gulf, the young often entering the bays. The spadefish consumes worms, crustaceans, and debris (Hildebrand and Schroeder, 1928), and the breeding season occurs during the "summer" in North Carolina (Hildebrand and Cable, 1938).

Station: 9A.

CICHLIDAE—Cichlid Family

Cichlasoma cyanoguttatum (Baird and Girard). Río Grande perch

Heros cyanoguttatus (Baird and Girard). Jordan and Snyder (1901, lagoons near Tampico)

Neetroplus carpintis Jordan and Snyder. Jordan and Snyder (1901, Laguna de Carpinte), Meek (1904, Valles, Rascón, Forlón), Jordan and Dickerson (1908, Tampico)

Cichlasoma cyanoguttatum (Baird and Girard). Meek (1904, Valles, Rascón, Forlón)

Herichthys cyanoguttatus Baird and Girard. Regan (1905, 1906–1908)

Cichlasoma laurae Regan. Regan (1908, Tampico)

Coastal lagoons and streams of southwestern Texas and northeastern Mexico, at least as far south as the Pánuco-Tamesí drainage.

The identity of C. *laurae* with *C. cyanoguttatum* has recently been confirmed by C. L. Hubbs after reexamination of Regan's specimens of *C. laurae* (personal correspondence with R. R. Miller, 1953).

The genus *Herichthys* was originally distinguished from the older *Cichlasoma* on the basis of the presence in its members of incisor-like rather than canine-like teeth. The variability of the tooth form, as well as other structures in the cichlids of this group, have been discussed by several authors, and Meek (1908) pointed out his reluctance to retain the genus *Herichthys* on the character of the dentition alone. C. L. Hubbs (1936) further noted the problems of arranging the American cichlids into genera, but he preferred to retain Regan's generic designation on a provisional basis. Certain recent authors (see, for example, Clark Hubbs, 1957, 1958) have reverted to Meek's policy of interpreting the genus *Cichlasoma* broadly, a practice which is followed here.

In the present study 778 specimens of this cichlid were taken from the headwater streams of the Río Tamesí, the Río Guayalejo, and the Laguna de Chairel. As revealed by observations and by its relative abundance in the various collections, this fish

thrives especially well in shallow lake-like conditions, and large populations were noted in the headwater lake of the Río Boquilla and in the Laguna de Chairel at Tampico. It also makes use of many stream habitats including pools and backwaters of the rivers and arroyos, and some schools even dwell in stream sections with slow to moderate current. Although generally abundant elsewhere, this cichlid was noticeably scarce in collections from the Río Mante. Juveniles were found to inhabit chiefly the shallow weedy backwaters. During the daytime the adults also forage extensively in the shallows, but at the slightest disturbance they retreat instantly to a predetermined haven in deeper water. There they often seek shelter in crevices under logs, in brush piles, and in caves beneath the banks among the cypress roots, a habit which apparently is shared by other members of the genus (see Meek, 1904). After vanishing into such holes among the roots, they generally reappear a moment later with just their heads protruding. At night this fish remains inactive in deeper water. This cichlid exhibits a wide range of tolerance for turbidity, depth, and bottom type. Judging by its abundance in the Laguna de Chairel and by previous reports of specimens from various coastal lagoons, it is probably tolerant also of at least mildly brackish water. Clark Hubbs (1951) has pointed out that the minimum temperature tolerance of this species near the northern limit of its distributional range is probably around 14°–15°C.

Cichlasoma cyanoguttatum is a gregarious species, and individuals were seldom observed alone. Each pool of the Arroyo Encino that was examined was found to have its resident school composed of all sizes from young to adults. In the Río Sabinas around Storms' Ranch several schools of mixed sizes were periodically observed, and each group seemed to remain within its own home area of the stream, normally characterized by a deep-water haven together with a shallow water browsing zone. In stream areas where no shallow water zone was available, the large stones and submerged cypress roots which formed the vertical walls of the stream apparently afforded sufficient exposed surface to satisfy the browsing habits of the resident cichlids. In the clear waters of the Nacimiento of the Río Sabinas a large school of about fifty adult individuals was often observed foraging among the roots of the sedges which grow at the origin of the river. A brush pile in deeper water about one hundred feet away provided shelter for the fishes when they were disturbed. Smaller individuals tended to remain in the marginal weeds at the river's origin. Mixed schools of this cichlid and the characin, *A. fasciatus*, were noted on a number of occasions.

The stomach contents of 20 specimens were analyzed. It was composed of about twenty-five per cent vegetation, five per cent small invertebrates, and the remainder primarily organic detritus. The vegetation included vascular plant matter (roots, stems, leaves, and seeds, as well as bits of *Chara* and spanish moss), filamentous fungus, filamentous algae (*Lyngbya, Oscillatoria, Hyalotheca, Mougeotia, Rhizoclonium, Spirogyra, Ulothrix*, and others), and occasional bottom diatoms (*Pinnularia*, an others). Insects made up the bulk of the invertebrates and included the aquatic larvae of Coleoptera and Diptera, as well as a large caterpillar and a scarabeid beetle, both of terrestrial origin. Water mites, cladocera, and protozoa also were noted. Intermixed with the flocculent detritus were small amounts of inorganic matter (rock, sand, and dirt).

In this cichlid a large pouch or bursa is connected with the anterior region of the

stomach. Although the contents are not listed in the above stomch analyses, the included material was generally the same as the stomach contents, but often in a better state of preservation. Bursas were found to contain, in addition to the above materials, fish eggs (about eighteen in one bursa) and fish skeletal parts (a complete skeleton in one bursa). This interesting structure functions as an accessory and, perhaps, preliminary storage sac for these wary fish which must often feed hurriedly in the exposed shallows. The fact that most of the consumed food materials are of relatively low energy content and nutritional value compels the fish to take in large quantities, thereby placing a premium on accessory storage facilities. The parallel with the rumen of certain terrestrial herbivores is obvious. From the condition of the contents in some specimens it appears that the bursa may also perform a digestive function.

This fish seems to feed all through the day, either picking around the bottom, nibbling at fungi, insects, or other material uncovered in the marginal vegetation, or scraping algae and detritus from the surface of submerged roots, stems, branches, or rocks. In feeding, this fish often employs a bird-like pecking behavior, frequently turning its head sideways to facilitate the scraping of materials from the submerged surfaces. In the possession of incisor-like teeth, general food habits, and behavior, this cichlid represents an interesting evolutionary parallel to the marine and estuarine sheepshead, *A. probatocephalus,* discussed elsewhere in the present paper.

Meek (1904) mentioned that females taken from the Río Purificacion on May 13th had immature ovaries, and he was unable to indicate the time of spawning. Specimens collected by the present writer on May 22nd revealed almost mature eggs which would apparently be ready for deposition in the latter part of June.

Fishes of the genus *Cichlasoma* seem to have excellent vision and, as noted above, they are quite wary. Meek (1904) aptly reported, "The species of this genus are very difficult to capture with a seine. They are more skillful in dodging a net, running around the end, or jumping over it, than are any other fishes I have ever collected." Success in capturing these cichlids may be enhanced by 1) employing a length of gill netting as a seine or using a seine possessing a long tapered bag in the center, 2) carefully observing the behavior of a school before attempting to capture the fish, and 3) maneuvering the net to a position between the fish and their deep-water haven, then pulling toward shore rapidly with as much splashing and confusion as possible. Turbid water collections tend to be more successful than clear water collections because of the reduced visibility. Both species of cichlids inhabiting the Arroyo Encino were successfully taken in fyke nets.

Stations: 1F,G,J,K,L,N; 2A; 3A,B,C,D,; 4A,B,D,E,G,K; 6A,B,C,D,E; 7B; 8A,B; 9A,B.

Museum Nos.: CNHM 4487, 4489, 62650, 62663, 62683; TU 5574, 5585, 5597, 5607, 5612, 5617, 5624, 5629, 5641, 5647, 5675, 5689, 5691.

Cichlasoma steindachneri Jordan and Snyder.

Cichlasoma steindachneri Jordan and Snyder. Jordan and Snyder (1901, Río Verde, Rascón), Meek (1904, Rascón, Valles, Forlón)

Known only from the Pánuco-Tamesí drainage system.

In the present study 365 specimens were obtained from the various headwater streams, the Río Guayalejo, and the Laguna de Chairel. Although fairly widespread, this fish was nowhere abundant in the collections, and its general distributional pattern

and habitat relations are not entirely clear. Its virtual absence from the Río Boquilla and the Adjuntas collection from the Río Guayalejo suggests that this fish may be intolerant of highly turbid conditions. Likewise, its presence throughout most of the Río Sabinas, the lower stretches of the Arroyo Encino, the Río Frío near the Nacimiento, and the Río Mante indicate that it is primarily a fish of clear water. This species is at home in lake-like conditions as evidenced by its relative abundance in collections from the reservoir of the Río Mante and from the Laguna de Chairel. In the Río Sabinas around Storms' Ranch this cichlid was found to inhabit backwaters, edges of moderate current, and even some riffle areas with swift current. Single subadult individuals, apparently referable to this species, were often observed among the rocks and boulders in strong current. Attempts to capture them proved futile because, when approached, they would simply disappear into a crevice between the rocks and reappear several feet away. Stomach analyses corroborate the above observations by clearly indicating that this fish consumes many riffle-dwelling species. Stomach analyses also confirm the fact that this cichlid forages extensively in the weedy backwaters.

C. steindachneri tends to be more solitary than the preceding species, and this is undoubtedly one of the chief factors responsible for its low density in the collections. This species may be even more wary than *C. cyanoguttatum*, however, a fact which would reduce not only its density in the collections, but also the frequency of observations. Fortunately, adults of *C. cyanoguttatum* are easily identified on sight, but due to the uncertainty of sight identification of small cichlids, most observations of the smaller individuals are not included here. A further complication arises from the fact that two other small cichlids, *Cichlasoma bartoni* (Bean) and *C. labridens* (Pellegrin), are known from the headwaters of the Río Pánuco (see Miller, 1956). Although these species have not yet been recorded from the Tamesí, they may be present, and some of the smaller cichilds observed, but not taken, may eventually turn out to be these species.

Stomach contents of 20 specimens were analyzed. Unlike the preceding species which feeds mainly on vegetation and detritus, *C. steindachneri* is chiefly carnivorous, preying upon a great variety of small invertebates. Snail remains (including *Cochliopa* sp., *Ferrissia* sp., and *Pachychilus* spp.) made up at least twenty per cent of the stomach contents; aquatic insects (larvae of Coleoptera, Diptera, Ephemeroptera, Neuroptera, Odonata, Trichoptera, and others) constituted forty-five per cent; miscellaneous invertebrates (spaeriid clams, cladocera, water mites, the amphipod, *Hyalella*, and the fresh-water shrimp, *Atya scabra*) three per cent; fish remains (eggs, larvae, fry, bones, scales) six per cent; filamentous algae (*Lyngbya, Gloeotrichia, Spirogyra*) five per cent, and undetermined organic matter and detritus mixed with mucus (much of which must have been snail remains) constituted the remainder. This fish is a very selective predator. The stomach of one 51 mm female, for example, contained over 100 chironomid larvae, 10 ceratopogonid larvae, 5 coleopteran larvae, 4 ephemeropteran larvae, a single small snail (*Cochliopa*), and a bit of detritus. Evidence that this cichlid fish feeds in the riffles rests upon the presence of riffle snails (*Pachychilus* spp.), riffle insects (larvae of psephenid beetles and certain Ephemeroptera, Neuroptera, and Trichoptera), and the small shrimp (*Atya scabra*) (see Darnell, 1956). Proof that it also feeds in the backwaters is provided by the presence

of sphaeriid clams, backwater snails (large numbers of *Cochliopa* sp. and some *Ferhissia* sp.), as well as certain backwater insects (especially the chironomids and ceratopogonids). The habitats of these invertebrates have been investigated in the general ecological study of the stream. It should be noted here that the snail-eating habits of this species are quite remarkable since not many fresh-water fishes are known to consume gastropods in such high percentage.

As in the previous species, a bursa is appended to the anterior region of the stomach, and this structure increases the storage capacity by about twenty-five percent. In most cases the bursas were found to be nearly empty, but they were occasionally loaded with the same types of materials as encountered in the stomachs. It is of interest to compare the relative gut lengths of the two species of cichlids discussed here. Although both may be considered omnivores, *C. cyanoguttatum*, which feeds largely upon detritus and vegetation, exhibits a gut length to standard body length ratio of about 2.5, whereas *C. steindachneri*, which consumes mainly invertebrates, displays a ratio of only about 1.2. These internal morphological features are of considerable ecological significance, as will be discussed elsewhere. It is possible that they will eventually prove valuable also as taxonomic characters, especially to aid in the separation of the very similar juvenile stages where the dentition and color patterns seem to be less distinctive.

In the Sabinas area spawning apparently occurs in April, and females above 100 mm taken during this month possessed mature ovaries containing thousands of tiny (0.55 mm) eggs, wereas females less than 70 mm had immature ovaries. On April 17, 1951 a number of hours were spent observing five females which were apparently constructing and guarding nests in a pool of the Arroyo Encino about 200 meters above its junction with the Sabinas. Each nest consisted of a chamber with two entrances excavated beneath large stones paving the bottom of the pool in water about 75 cm in depth. While a male stood by, about 20 cm above and to one side of each nest, the very busy females spent most of their time within the chambers, coming out briefly, now and then, to chase away the numerous interested spectators. These intruders included adult *C. cyanoguttatum* (both sexes) and the characin, *A. fasciatus*, which were waiting less than a meter away in deeper and shallower water, respectively, and thoroughly engrossed in all proceedings. Three males and a single female (102 mm) were taken for identification (with a span of gill-netting for a seine) and constitute collection II. Examination revealed that the ovaries of the female were very ripe, but spawning had apparently not yet begun.

Stations: 1G,I,J,K,L,N; 2A; 3A,B,C; 4B,C,D,E,G,I,J,K,L; 5A; 6B,D; 7B,C,D; 8A,B; 9B.

Museum Nos.: CNHM 4488, 62651, 62662, 62671, 62682; TU 5577, 5586, 5593, 5598, 5603, 5626, 5640, 5652, 5667, 5674, 5677, 5686, 5692.

Eleotridae—Sleeper Family

Dormitator maculatus (Bloch). Fat sleeper

Along Atlantic coast of the Americas from North Carolina to Brazil and throughout the West Indies.

The fat sleeper is recorded from the Río Tamesí for the first time on the basis of twenty small specimens taken from the Laguna de Chairel at Tampico. Although

Meek (1904) stated that this sleeper usually inhabits salt or brackish water, its residence in fresh water also has been well substantiated (Gunter, 1942, 1956; Carr and Goin, 1955). The present writer has taken adult specimens in southern Louisiana from shallow densely-vegetated fresh-water pools of the Bonnet Carré spillway a few hundred yards from the Mississippi River.

Station: 9B.

Museum No.: TU 5643.

Elotris pisonis (Gmelin). Spinycheek sleeper, Guavina, Tetard

Eleotris abacurus Jordan and Gilbert. Jordan and Dickerson (1908, lagoon near Tampico)

Atlantic coast of the Americas from South Carolina to Brazil; also reported from the West Indies.

Pending revision of the group certain recent writers (including Bailey *et al.* 1954) have employed the older name, *E. pisonis* (Gmelin), for the "sole mainland representative of the genus in eastern United States." For this reason in the present work *E. abacurus* is provisionally included as a synonym of *E. pisonis*. This sleeper is known to inhabit brackish waters and fresh-water streams connected with brackish water (Carr and Goin, 1955).

Station: 9A.

Gobiomorus dormitor Lacépède. Bigmouth sleeper, Metapíl

Philypnus dormitor (Lacépède). Jordan and Snyder (1901, lagoons near Tampico), Meek (1904, Rascón, Valles, Forlón)

Gobiomorus dormitor Lacépède. Jordan and Dickerson (1908, Tampico), Darnell (1955, Tamesí)

Coastal streams and lagoons of the Atlantic coast from Florida and southern Texas to Dutch Guiana; also found in Cuba, the Bahamas, and throughout the West Indian islands.

In the present study 11 specimens were taken from the Arroyo Encino, the Ríos Sabinas, Mante, and Guayalejo, and the Laguna de Chairel at Tampico. In addition, numerous day and night observations were made in the lower portions of the Arroyo Encino and in the Río Sabinas around Storms' Ranch.

Hildebrand (1938) reported that in Panamá this fish is common in brackish and fresh-water lowland swamps and streams, and that it also ascends rivers in which it occupies shallow weedy coves. In the Tamesí drainage, as indicated, it was found to occupy a wide variety of habitat types, even in the headwaters. The species is a solitary bottom dweller. It normally lives in clear pools and backwaters, but it tolerates a slight current and a fair amount of turbidity. Silt is the preferred bottom type, and the metapíl was often seen to conceal itself effectively by fanning this material with its enlarged pectoral fins, thereby covering all but the dorsally-placed eyes with silt. This fish was captured in water from a few centimeters in depth (in the Arroyo Encino and Río Sabinas) to at least three meters in depth (in the reservoir of the Río Mante), and specimens were taken by seine, fyke net, and spear. The metapíl frequently creeps along the bottom on its enlarged pectoral fins, but it also darts with a quick tail movement, and it is capable of rapid and sustained swimming. As previously noted (Gunter, 1942, 1956; Darnell, 1955) this species is clearly euryhaline. The remarkable nocturnal terrestrial forages of this gobioid fish on the rocky beaches of

the Río Sabinas around Storms' Ranch have been described by the present writer (Darnell, 1955). Miller (1959) has recently discussed the systematics, distribution, and ecological relations of the three known species of this genus.

Limited food studies indicate that the metapíl is highly predatory, feeding upon a variety of small fishes and both aquatic and terrestrial arthropods (Darnell, 1955). In the backwater community of the Río Sabinas and Arroyo Encino this is certainly one of the top predatory species.

Nothing seems to have been reported regarding the spawning habits of this fish. According to Robert Miller (personal correspondence) it is known to live and reproduce in the big inland fresh-water Lago de Yojoa in Honduras, and Schultz has recorded a very small (18 mm) specimen from apparently fresh water in Venezuela. Nevertheless, the sleepers are basically littoral marine fishes, and *G. dormitor* itself is known to be euryhaline. In the absence of objective information to the contrary, it seems plausible to assume that this species breeds primarily in brackish-water lagoons and estuaries (as *D. maculatus* seems to do). On these grounds the metapíl is tentatively considered to be catadromous, like the mountain mullet. As pointed out by Myers (1949b), however, the application of the term might hinge upon how far into brackish or salt water a species must go to be called catadromous.

Stations: 1J,K,N; 4D,G,J; 7D; 8A,B; 9A,B.

Museum Nos.: CNHM 4490, 62687, 62689; TU 5644, 5661, 5694.

Gobiidae—Goby Family

Evorthodus lyricus (Girard). Lyre goby

Evorthodus breviceps Gill. Jordan and Dickerson (1908, lagoon near Tampico)

Evorthodus lyricus (Girard). Ginsburg (1931)

Along Atlantic coast of the Americas from Chesapeake Bay south to Surinam; common throughout the West Indies.

The lyre goby has been reported by Meek and Hildebrand (1928) to enter fresh water, but its preferred habitat on the Louisiana coast appears to be the mud-bottomed tidal lagoon (Ginsburg, 1931).

Station: 9A.

Gobionellus boleosoma (Jordan and Gilbert). Darter goby

Rhinogobius shufeldti Jordan and Eigenmann. Jordan and Dickerson (1908, lagoon near Río Pánuco) (in part)

Gobionellus boleosoma (Jordan and Gilbert). Ginsburg (1932)

Atlantic coast of North America from North Carolina south at least to Panamá, and possibly to Brazil; also present in Cuba.

According to Ginsburg (1932) the darter goby ranges from salt to brackish water, but Hildebrand and Cable (1938) indicated that *G. boleosoma*, as well as *G. bosci* may live and apparently breed in a small pond near Beaufort, North Carolina, which ranges from brackish to nearly fresh water. Hildebrand and Cable (1938) also discussed the spawning and early development of the darter goby, and Gunter (1945) reported taking ripe females in southern Texas in November.

Station: 9A.

Gobionellus claytoni (Meek).

Rhinogobius shufeldti Jordan and Eigenmann. Jordan and Dickerson (1908) (in part)

Gobionellus claytoni (Meek). Ginsburg (1932)

East coast of tropical America, probably from Tampico, but definitely from Vera Cruz, Mexico south to Panamá; also known from Cuba and Trinidad.

Ginsburg (1932) recognized two species in the Tampico material which Jordan and Dickerson (1908) had called *Rhinogobius shufeldi* Jordan and Eigenmann. Although most of the specimens were referred to *Gobionellus boleosoma* (Jordan and Gilbert), a single specimen belonged to a different species, apparently, but not definitely, *Gobionellus claytoni* (Meek), which had previously been known from Vera Cruz on the eastern coast of Mexico. This record is, thus, in need of verification. Meek (1904) noted that this goby inhabits both fresh and brackish waters on the coast of Vera Cruz.

Station: 9A.

Gobiosoma bosci (Lacépède). Naked goby

Gobiosoma bosci (Lacépède). Jordan and Dickerson (1908, no locality), Ginsburg (1933)

Atlantic coast of North America from Massachusetts south at least as far as Tampico (and possibly to Vera Cruz), Mexico.

The naked goby seems to prefer shallow grassy flats and marsh pools (Gunter, 1945; Reid, 1954; Kilby, 1955). It has been taken from a wide range of salinities, mostly below 20 ‰, and Hildebrand and Cable (1938) and Bailey *et al.* (1954) noted specimens from fresh water in the spring. Spawning and development of the young in a small land-locked pond near Beaufort, North Carolina has been reported by Hildebrand and Cable (1938), and Gunter (1945) suggested that in southern Texas the breeding season probably extends from spring to fall.

Station: 9A.

Bothidae—Flatfish Family

Citharichthys spilopterus Günther. Bay whiff, Sand dab

Citharichthys spilopterus Günther. Jordan and Dickerson (1908, Tampico)

Atlantic coast of the Americas from New Jersey south to Brazil; found in Cuba and throughout the West Indies.

This catfish is known to enter fresh water (Gunter, 1942), and Gunter (1945) took specimens from the bays of southern Texas at salinities ranging from 2.5 ‰ to 36.7 ‰. According to Hoese (1958) this is the common bay and inshore dab of the Texas coast.

Station: 9A.

Batrachoididae—Toadfish Family

Opsanus beta (Goode and Bean). Gulf toadfish

Opsanus tau (Linnaeus). Jordan and Dickerson (1908, Tampico)

Throughout the Gulf of Mexico.

Hoese (1958) indicated that *Opsanus beta* (Goode and Bean) is the common toad-

fish of the Texas coast, hence the Tampico record probably refers to the latter rather than to *O. tau*.

Station: 9A.

Zoogeographic Discussion

Several authors have discussed the zoogeographic relations of the fresh-water ichthyofauna of eastern Mexico. Meek (1904) divided the country into five "fish faunal areas," and he included all of eastern Mexico (as well as southern and southwestern Mexico) in one large faunal area characterized by "tropical fishes." He pointed out, however, that the east coast streams contained many species belonging to northern families and that of the thirty-two species then known from the Pánuco-Tamesí basin, fifteen represent northern elements. On the basis of the same information, Regan (1906–08) divided the fresh-water fishes of eastern Mexico into two "Provinces." The northernmost, or Río Grande Province, was said to extend from southern Texas to central Vera Cruz, whereas the southern, or Guatemalan Province, included all of southern Mexico (on both coasts) and extended into Central America. The Pánuco-Tamesí system, therefore, was included in Regan's Río Grande Province. In 1909 Eigenmann, who had worked mainly with South American fishes, divided the fresh-water ichthyofauna of the Americas south of the Tropic of Cancer into four distinct faunal areas. The northernmost, extending from the Tropic of Cancer to the Isthmus of Tehuantepec, was termed by him the "Transition Fauna." Eigenmann pointed out that the ichthyofauna of the Río Grande, above the area, is distinctly northern, and that the fauna of the Río Papaloapan, below the area, is as distinctly tropical, "although the former contains a few southern elements, and the latter a few northern ones." In between these two systems, the Transition Fauna was noted to be characterized largely by intrusive elements from both the north and the south. He pointed out further that, "It is of comparatively recent origin and not an independent fauna but a mixture of the advance guards of the North American and South American faunas."

De Buen (1947) summarized the works of the previous authors, and he proceeded to divide eastern Mexico into three ichthyogeographic regions, the "Provincia del Bravo" on the north, the "Región Neotropical" on the south, and the "Banda de Transición" in between. The Band of Transition, in which both the northern and the southern elements are well represented, was found to be distinguishable in both the Atlantic and Pacific coast drainages, thereby forming an irregular but continuous band entirely traversing the continent and located mainly below the Tropic of Cancer. On the Atlantic coast it was noted to include only the Pánuco-Tamesí drainage and neighboring coastal lagoons and was designated by De Buen (1947) as the Pánuco Province. He subdivided this province into three "sections," as follows.

Tampico section.—Lower part of the Ríos Pánuco and Tamesí, with the neighboring coastal lagoons;

Valles section.—Ríos Verde, Frío, and Tampaón, affluents of the Río Pánuco, and the middle and upper part of the Tamesí drainage;

Moctezuma section.—The upper (Río Tula) and middle (Río Moctezuma) tributaries of the Río Pánuco, and also the affluent Santa María.

Darlington (1957) has discussed the broader aspects of the zoogeographic relations of the fresh-water ichthyofauna of North, Central, and South America. Although he was

not specifically concerned with the details of the fishes of particular streams of eastern Mexico, much of his analytic discussion is relevant and will be brought up later in connection with the origins of the ichthyofauna of the Río Tamesí.

In summary, it may be stated that among the fresh-water fishes of eastern Mexico some tropical elements are known to penetrate as far north as southern Texas, some of the northern elements penetrate as far south as Central America, but the Pánuco-Tamesí system, containing roughly equivalent numbers of species of northern and southern origin, represents the area of greatest overlap. The significant portion of any zoogeographic treatment is the analysis, and logically this should precede the naming stage. For this reason the present writer prefers to withhold judgment on the naming of ichthyofaunal regions until this obviously transitional area is subjected to far more critical study.

Zoogeographic relations of the estuarine and littoral marine fish fauna of the Mexican east coast have received little attention. Although the shallow water fishes of the northern and southern shores of the Gulf have long been recognized as being largely distinct, details of the transition zone along the western Gulf have not been studied. Gunter (1952) pointed out that the majority of published distributional records on Atlantic coast fishes which mention the Gulf of Mexico at all, end at the Río Grande, creating the impression that a sudden faunal barrier is encountered at that point. He noted further that, whereas a faunal break does occur further down on the Mexican east coast, the shallow water area from the border to about the region of Tampico contains more or less the same general faunistic picture as the Texas coast which has become well known in the past few years. For example, the lagoons north of Tampico yield annually thousands of pounds of black drum, speckled trout, and redfish, as well as many croakers and brown shrimp. Hildebrand (1955), likewise, indicated that along the Mexican east coast the shallow water fauna changes from north to south, and although many of these changes are gradual, the main break probably occurs in the vicinity of Tampico. This is reflected in the commercial fishery from one relying predominantly on the croakers and weakfishes (Sciaenidae) to one producing many robalos (Centropomidae) and mojarras (Gerridae).

Ginsburg (1952) has noted a similar, although less pronounced, transition in the shallow water fish fauna of the Florida west coast, and he has aptly pointed out that faunas may be distinguished, not only by differences in species composition, but also by differences in relative species abundance. The west coast of Florida, like the east coast of Mexico, contains elements of a disjunct northern or "Carolinean" fauna (characteristic of the south Atlantic and northern Gulf states, but broken by peninsular Florida) and a wide-ranging southern or "Caribbean" fauna (characteristic of Cuba, the West Indies, and Central America). Information regarding the marine invertebrate communities of eastern Mexico is scarce, but Hildebrand (1954, 1955), Rehder (1954), and others have noted that a somewhat parallel faunal change probably exists. The marine algae and vascular plants of the area are too poorly known for comment (Taylor, 1954; Thorne, 1954).

The matter of zoogeography is basically a problem of the ecological relations of individual species. It deals with their respective abilities to cross barriers, to adapt themselves to new physical environments, to withstand new predators and parasites, and to compete successfully with other species which are, to a greater or less degree, partial

ecological equivalents. Unfortunately, too little is known about the systematic status, relative abundance, actual geographic range, and ecological relations of many of the fresh-water and euryhaline fishes of eastern Mexico to permit a definitive treatment of their ecological zoogeography at the present time. Enough information is at hand, however, to sketch out some of the major features of these relations, and although future work will be necessary to establish the details, the overall patterns discernible at the present time should not be materially modified by future work.

Consideration of the zoogeographic relations of the fishes of the Río Tamesí and related coastal waters will be greatly facilitated by an analysis of the salinity relations of the species based upon the best information currently available. Any classification of fish species based upon salinity tolerances is, of course, arbitrary, since sharp dividing lines are not found in nature, and all intergradations are known. Myers (1938, 1949a) has found it convenient for purposes of zoogeographic analysis to designate certain families as primary fresh-water fishes, others as secondary fresh-water fishes. These concepts have been broadened by Darlington (1957) and redefined approximately as follows. *Primary division* forms consist of families or other groups which are presently restricted to fresh water and whose recent ancestors also were probably so restricted. *Secondary division* forms are those families or other groups which, although they occur chiefly in fresh water, can enter the sea and survive there, or they recently descended from ancestors which could do so. According to these concepts the present distributions of primary division fishes are the results of dispersal through fresh water, whereas the present distributions of secondary division fishes may be explained partly as a result of coastwise dispersal through brackish or even marine waters. Bailey *et al.* (1954) conceded the value of these terms for descriptive zoogeographic purposes, but they pointed out that certain species do not necessarily respect family lines and that such exceptional forms would permit local movement through bays and brackish marshes of members of primary division families. They also found exceptional cases where members of secondary division families were apparently restricted to fresh water. Thus, the general thesis of Myers (1938, 1949a) must be interpreted with caution when applied to a given species.

Bailey *et al.* (1954) and Gunter (1956) have also pointed out that distributional records unaccompanied by actual bottom salinity measurements should be accepted with caution when attempting to describe salinity tolerances of a fish species. Every effort is made herein to use only reliable information as discussed in the preceding text. It should be kept in mind that salinity *occurrence*, as indicated by distribution records, is not necessarily equatable to the actual salinity *tolerance* of a fish species, and, as noted by Krogh (1939) and others, some species may diverge widely in this regard. The use of the term "apparent salinity tolerance" is suggested for cases where actual experimental evidence is unavailable.

The present arrangement of salinity tolerance categories is identical with the simple and logical classification presented by Bailey *et al.* (1954) except that the numerical and letter headings of the outline have been modified to bring them into greater conformity with conventional usage. Also, the strictly fresh-water species are divided into primary and secondary division categories to emphasize the historically different backgrounds of these groups in the Tamesí fauna. Only one species common to the present list and that of Bailey *et al.* (1954) has been placed in a different salinity tolerance cate-

gory. This species, *Fundulus grandis*, has been shifted on the basis of additional habitat information presented by Miller (1955) and discussed earlier in this paper. In the following classification the letters in parentheses following the species names relate to their zoogeographic affinities as follows: *N*, the family to which the species belongs is primarily northern; *S*, the family to which the species belongs is primarily southern; *S–N*, a northern representative of a southern family; *N–S*, a southern representative of a northern family; *E*, the species involved is considered to be endemic in the Pánuco-Tamesí system.

Provisional Classification of Río Tamesí Fishes Based on Apparent Salinity Tolerance

I. Fresh-water species.

A. Strictly fresh-water. Presence at station 9B is not considered sufficient evidence alone to exclude a species from this category. (15 species)

1. Primary division (*sensu* Darlington, 1957).

Ictiobus bubalus (N)
Dionda rasconis (N,E)
Dionda sp. (N,E)
Notropis lutrensis (N)
Notropis sp. (N,E)
Ictalurus australis (N–S)
Ictalurus mexicanus (N,E)

2. Secondary division (*sensu* Darlington, 1957).

Gambusia panuco (S,E)
Gambusia regani (S,E)
Gambusia vittata (S,E)
Gambusia sp. (S,E)
Mollienesia latipunctata (S,E)
Xiphophorus montezumae (S,E)
Xiphophorus variatus (S,E)
Cichlasoma steindachneri (S,E)

B. Facultative invaders of brackish water.

1. Sporadic invasion by stragglers into waters of low salinity (*i.e.*, at least 4.5 ‰). (4 species)

Astyanax fasciatus (S)
Mollienesia formosa (S) (placement provisional)
Mollienesia sphenops (S)
Cichlasoma cyanoguttatum (S)

2. Frequent invasion, probably for a considerable time, into water of low salinity (*i.e.*, at least 4.5 ‰); maximum tolerance (or preference) for salinity presumably greater than B-1. (4 species)

Lepisosteus osseus (N)
Lepisosteus spatula (N)
Ictalurus furcatus (N)
Gambusia affinis (S–N)

II. Euryhaline species. Fishes with a wide range of tolerance to salinity.

A. Anadromous fishes. Entering fresh water to breed; some are at times residual in fresh water. Commonly entering water of high salinity. (4 species)

Dorosoma cepedianum (N)
Dorosoma petenense (N)
Dormitator maculatus (S)
Eleotris pisonis (S)

B. Catadromous fishes. Entering the sea to breed. (2 species)

Agonostomus monticola (S)
Gobiomorus dormitor (S) (placement provisional)

C. Marine or brackish-water fishes that invade strictly fresh water.

1. Frequent invasion, often for a considerable time and distance; some species occasionally residual in fresh water. (5 species)

Anchoa mitchilli (S–N)
Oostethus lineatus (S)
Mollienesia latipinna (S)
Mugil cephalus (S)
Mugil curema (S)

2. Sporadic invasion, probably for a brief period and usually for a short distance. Most often not exceeding tidal water. (9 species)

Cyprinodon variegatus (S)
Fundulus grandis (S–N)
Fundulus similis (S–N)
Lucania parva (S–N)
Eucinostomus melanopterus (S) (placement provisional)
Evorthodus lyricus (S) (placement provisional)
Gobionellus boleosoma (S)
Gobionellus claytoni (S)
Gobiosoma bosci (S–N)

D. Marine species. Facultative invaders of water of moderate to low salinity. Not entering fresh water (probable temporary stragglers, especially young fish, excluded). (17 species)

Carcharhinus leucas (S)
Anchoa hepsetus (S)
Galeichthys felis (S–N)
Caranx hippos (S)
Caranx latus (S)
Lutjanus cyanopterus (S)
Lutjanus griseus (S)
Archosargus probatocephalus (S)
Eugerres brasilianus (S)
Eugerres plumieri (S)
Bairdiella ronchus (S)
Cynoscion nebulosus (S–N)
Micropogon undulatus (S–N)
Pogonias cromis (S)
Chaetodipterus faber (S)
Citharichthys spilopterus (S)
Opsanus beta (S–N)

Among the 15 species of strictly fresh-water fishes obtained from the Río Tamesí, seven (*I. bubalus, D. rasconis, Dionda sp., N. lutrensis, Notropis sp., I. australis,* and *I. mexicanus*) belong to northern families, and eight (*G. panuco, G. regani, G. vittata, Gambusia sp., M. latipunctata, X. montezumae, X. variatus,* and *C. steindachneri*) are representatives of southern families. As presently considered, all of these species are endemic in the Pánuco-Tamesí system except the sucker (*I. bubalus*) and the minnow (*N. lutrensis*) which are northern species and the catfish (*I. australis*) which is a southern representative of a northern family. All seven of the northern species belong to primary division families, and all eight of the southern species are secondary division forms.

Of the fresh-water species which sporadically invade low salinity waters, all four are of southern affinity. One of these (*A. fasciatus*) is widely distributed on both slopes of tropical America. Two of the species (*M. formosa* and *C. cyanoguttatum*), although representatives of southern families, are Tamaulipan in distribution, *i.e.*, they range from the Pánuco-Tamesí system north through the coastal waters of the Mexican state of Tamaulipas and through the Tamaulipan biotic province of southern Texas (see Clark Hubbs, 1957). The one remaining species (*M. sphenops*) is widespread in eastern Mexico, but (according to Carl Hubbs in personal correspondence) in the northern portion of its range (from the Río Pánuco, north), it is considerably differentiated and may eventually be recognized as taxonomically distinct.

Of the four fresh-water forms which invade low salinity water for a considerable period of time, three species (*L. osseus*, *L. spatula*, and *I. furcatus*) belong to northern families, and the remaining form (*G. affinis*) is a northern representative of a southern family. These four species are all common along the northern Gulf coast, and all four apparently reach their southern distributional limits in the Pánuco-Tamesí system. *I. furcatus* represents a primary division family, but it unquestionably belongs in the present category.

In summary, of the 23 species of fresh-water fishes so far recognized from the Río Tamesí, 10 belong to northern families, and 13 are of southern affinity. All but three of the strictly fresh-water species are endemic, but the facultative invaders of brackish water are all more widespread. Only one of the northern species and two of the southern forms are known to range south of the Pánuco-Tamesí system, but at least five of the northern species and five of the southern forms range north of the area. Not only do the southern forms predominate in numbers, but they also appear to be better differentiated morphologically, and hence taxonomically, a fact which should become progressively clearer as the groups become better known. Present information suggests that the Pánuco-Tamesí system was invaded early by southern forms at a time when the northern barrier was rather effective. Since the early invaders were all secondary division forms, however, they may have dispersed northward along the Mexican coast to the Pánuco-Tamesí system through brackish or fully marine water. More recently the faunal connection with the north has increased while penetration from the south has probably been reduced. This fluctuation in the effectiveness of barriers to coastwise dispersal of the fresh-water fishes undoubtedly reflects, in part, the extent and degree of freshness of the coastal lagoons both above and below the Tampico area. These factors, in turn, relate to the water level of the Gulf of Mexico as well as to certain processes of erosion and barrier beach construction (see discussion by Hedgpeth, 1953).

The euryhaline forms present a different zoogeographic picture. Among the four anadromous species two (*D. cepedianum* and *D. petenense*) are northern, and the others (*D. maculatus* and *E. pisonis*) are southern. One of the northern species (*D. cepedianum*) reaches its southern limit in the Pánuco-Tamesí system, but the other three are widespread on the Mexican east coast. Both of the catadromous species (*A. monticola* and *G. dormitor*) are wide-ranging southern forms. The former appears to be rare above the Tamesí area, but the latter is found in streams of southern Texas.

All five of the euryhaline species which frequently invade fresh water belong to southern families. Two (*A. mitchilli* and *M. latipinna*) are northern species which extend only as far south as Yucatán. The remaining three (*O. lineatus*, *M. cephalus*, and *M. curema*) are more widespread.

Of the nine euryhaline forms which sporadically invade fresh water, all represent southern families. Four (*F. grandis*, *F. similis*, *L. parva*, and *G. bosci*) apparently reach southern distributional limits in the Tampico area. Three of these species belong to the family Cyprinodontidae which, as indicated by Darlington (1957), is primarily tropical (although the particular genera are northern, as will be pointed out below). A single southern species (*G. claytoni*) achieves its northern limit in eastern Mexico, probably around Tampico. The remaining four (*C. variegatus*, *E. melanopterus*, *E. lyricus*, and *G. boleosoma*) are widespread coastal forms.

All 17 of the marine species which occasionally enter low salinity water also belong

to southern families. Four of these species (*L. cyanopterus*, *E. brasilianus*, *E. plumieri*, and *B. ronchus*) have not been taken north of Tampico. Four (*G. felis*, *C. nebulosus*, *M. undulatus*, and *O. beta*) are considered to be northern representatives of southern groups, but only one of them (*C. nebulosus*) achieves its southern distributional limit around Tampico. The remaining nine species (*C. leucas*, *A. hepsetus*, *C. hippos*, *C. latus*, *L. griseus*, *A. probatocephalus*, *P. cromis*, *C. faber*, and *C. spilopterus*) are wide-ranging on the western and northern Gulf coasts.

In striking contrast with the fresh-water fauna, the euryhaline fishes are overwhelmingly southern in derivation (at the family level). Only two of the 37 recognized species represent northern families; the remainder are of southern affinity. Ten of the species, however, although representing southern families, belong to genera or species whose distribution is largely northern, and these may be considered part of a poorly differentiated northern fauna. Seven of the 12 northern euryhaline forms apparently reach southern distributional limits in the Tampico area, but only five of the 25 southern species seem to reach northern limits here. No endemism among the euryhaline forms has been noted.

Darlington (1957) has called attention to the existence of two great centers of evolution and dispersal of fresh-water fishes in the Americas, the southern center in the Amazon River basin in South America and the northern center in the Mississippi River basin of North America. The intervening drainage systems are marked by progressive subtractions of the fresh-water elements (and especially of the primary division fishes). The advance guards of the two faunas overlap in the region from Guatemala to southern Texas, but most of the streams of Central America and Mexico are depauperate of truly fresh-water forms of Amazonian or Mississippian origin. The Amazonian fauna is represented in the Río Tamesí only by the Cichlidae (with two species) and the Characidae (with a single species). Among these, only the characin belongs to a primary division family (providing, however, an excellent example of why Myers' family salinity tolerance categories must be applied with caution). The remaining fresh-water inhabitants of the Río Tamesí of southern affinity are all members of the family Poeciliidae (ten species), a secondary division group, and they represent a southern family which has undergone most of its evolution in Central America and Mexico. Representatives of the Mississippian fresh-water fauna which have reached the Tamesí include the Catostomidae (one species), Cyprinidae (four species), and Ictaluridae (three species), which are primarily division families, and Lepisosteidae (two species), which is a secondary division family.

Although the fresh-water fishes of the Río Tamesí include 10 representatives of the Mississippian fauna, the absence of many other species (which are abundant in southern Texas) is striking. Of especial interest is the absence of many cyprinids and all centrarchids and percids. The fact that the southern fishes have not been overwhelmed by the pressure of invaders from the north undoubtedly reflects, in large degree, the continued effectiveness of the salinity barrier during the late Tertiary.

Examination of the habitats of the northern and the southern elements of the fresh-water fish fauna of the Tamesí drainage reveals a striking and curious ecological correlation. The fish species which inhabit the small upstream waters such as springs, arroyos, and backwaters of the smaller rivers are almost entirely southern in derivation. These include the various poeciliids as well as the characin and the two cichlids. Except for

the ubiquitous characin these are all secondary division fresh-water fishes. Partial exceptions are encountered in the two species of *Dionda* and one of *Notropis*, which, although northern, seem to be invading the domain of the tropical forms. On the other hand, those fish species which inhabit the deeper waters, the larger rivers, and downstream habitats, in general, are largely of northern origin. These include the gars, suckers, shiners, and catfishes, and they are mostly primary division fresh-water fishes. Partial exceptions include the characin and cichlids, species of wide habitat tolerance. In other words, among the fresh-water fishes of the Tamesí drainage, the primary division northern elements have not contributed materially to the upstream communities, and the secondary division southern elements apparently have not contributed materially to the community of the larger rivers.

Explanation of these phenomena may rest in the nature of the parent faunas and of the salinity barriers. The upstream fishes of southern origin appear to have arrived earlier. They probably have been derived from brackish-water ancestors, but they may have entered the Tamesí as fresh-water fishes at a time when the coastal lagoons were rather fresh. In either event, the absence of downstream forms of southern origin undoubtedly is a reflection of the fact that the waters of tropical America have not developed a large-river fish fauna, and such forms simply were not available from the south. On the other hand, the fish fauna of southern Texas includes ample species which might occupy both the upstream and the downstream habitats of the Tamesí (see Clark Hubbs, 1957, 1958, and Robinson, 1959). In this case it is probable that only the large-river fishes have been able to traverse the salinity barrier (perhaps, by accidental dispersal in times of flood).

As pointed out by Gunter (1956) and others, many widespread marine fishes tend to enter fresh water in the tropical portions of their ranges, and many marine species which are essentially limited to the tropics also invade fresh water, some populations having become established there. The presence of the marine element is one of the striking characteristics of the American tropical fresh-water fish fauna, and in the Río Tamesí this element is represented by several species (*G. dormitor*, certain mugilids including *A. monticola*, and probably a number of other forms for which present evidence is less conclusive). Isolated from the northern fresh-water fauna, these marine invaders seem to have partially filled existing ecological vacua. Such forms have been termed by Myers (1949a) "complementary" fishes because their distributions are largely complementary to those of the primary and secondary division forms. It is interesting to note that the tropical marine derivatives which are present in the Tamesí appear to be primarily inhabitants of the larger waters, and this list will undoubtedly grow as the larger streams are more thoroughly studied.

The case of the euryhaline fishes of the Mexican east coast is just the reverse of that of the fresh-water forms. As noted above, the coasts of eastern and southern United States may be considered only a secondary center of faunal differentiation. The southern center, however, including the West Indies and Central America, has produced an abundant and varied tropical marine inshore fish fauna, far richer than that of the north. The southern center has, in fact, given rise to most of the genera and species which characterize the shallow-water ichthyofauna of the northern Gulf. Whereas salinity barriers are of great importance in determining the coastwise distribution of fresh-water species, they are of relatively minor import for the euryhaline forms. The fact

that a transition zone for the euryhaline species in the vicinity of Tampico does occur suggests the operation of other factors. Here the problem appears to be not so much a matter of dispersal as it is a matter of ecology, that is, the relative abilities of the northern and the southern forms to adapt and to compete in a complex north-south gradient of habitat features involving such factors as water currents, seasonal temperatures, bottom types, etc. (see Leipper, 1954; Lynch, 1954; Price, 1954; and Taylor, 1954). As mentioned earlier, the situation is in some respect comparable to that existing on the west coast of Florida and which has been summarized by Reid (1954) as follows, "the transition from the temperate fauna of the northern Gulf coast to the tropical, West Indian complex of the southern Gulf coast of Florida is a gradual one in which the southern forms begin to appear somewhat irregularly and seasonally while the species density of the northern fishes decreases." On the Mexican east coast the north-south transition is probably more abrupt, but before a clear picture of the distributional relations of the euryhaline and littoral marine fauna of this area is available a great deal of further work must be accomplished.

Summary

In the present study a total of 11,043 specimens of fishes was obtained in 66 collections from the tributaries of the Río Tamesí and from a coastal lagoon near Tampico. On the basis of these collections and literature reports, 60 species of fishes are now recognized from the area, 23 of which are fresh-water forms and 37 of which are considered to be euryhaline. These include the following: *Carcharhinus leucas, Lepisosteus osseus, L. spatula, Anchoa hepsetus, A. mitchilli, Dorosoma cepedianum, D. petenense, Astyanax fasciatus, Ictiobus bubalus, Dionda rasconis, Dionda* sp., *Notropis lutrensis, Notropis* sp., *Galeichthys felis, Ictalurus australis, I. furcatus, I. mexicanus, Oostethus lineatus, Cyprinodon variegatus, Fundulus grandis, F. similis, Lucania parva, Gambusia affinis, G. panuco, G. regani, G. vittata, Gambusia* sp., *Mollienesia formosa, M. latipinna, M. latipunctata, M. sphenops, Xiphophorus montezumae, X. variatus, Agonostomus monticola, Mugil cephalus, M. curema, Caranx hippos, C. latus, Lutjanus cyanopterus, L. griseus, Archosargus probatocephalus, Eugerres brasilianus, E. plumieri, Eucinostomus melanopterus, Bairdiella ronchus, Cynoscion nebulosus, Micropogon undulatus, Pogonias cromis, Chaetodipterus faber, Cichlasoma cyanoguttatum, C. steindachneri, Dormitator maculatus, Eleotris pisonis, Gobiomorus dormitor, Evorthodus lyricus, Gobionellus boleosoma, G. claytoni, Gobiosoma bosci, Citharichthys spilopterus,* and *Opsanus beta.* The known distribution of species within the drainage is as follows: Río Sabinas (16 species), Río Frío (13), Río Mante (10), Río Guayalejo (20). and the coastal lagoons and other areas around Tampico (45). For each species of fish information is given, as currently available, regarding the following points: nomenclature, distribution, salinity relations, general ecology, food habits, and reproduction.

Salinity relations of the Río Tamesí fishes are analyzed as a basis for zoogeographic discussion. The 23 fresh-water species include strictly fresh-water forms (15), sporadic invaders of low salinity water (4), and frequent invaders of low salinity water (4). The 37 euryhaline species include anadromous forms (4), catadromous forms (2), frequent invaders of fresh water (5), sporadic invaders of fresh water (9), and marine species which are facultative invaders of low salinity water (17). Twelve of the species are

considered to be endemic in the Pánuco-Tamesí system, all of which are strictly fresh-water forms.

For both the fresh-water fishes and the littoral marine fishes, eastern Mexico represents a zone of transition between the temperate and the tropical faunas. Although the most intensive area of overlap for both the fresh-water and the marine groups appears to occur at about the level of Tampico, the problems of the two groups appear to be somewhat different. Among the fresh-water species of the Tamesí representatives of southern families slightly outnumber representatives of northern families (13:10). Among the euryhaline species representatives of southern families greatly predominate over those of northern families (35:2). Ten of the euryhaline forms, however, are northern representatives of tropical families, and considered at this level the southern species are only about twice as numerous as species of northern distribution (25:12). Analysis of habitat distribution of the fresh-water fishes of the Tamesí reveals that those of southern derivation inhabit primarily the small upstream waters, whereas those of northern affinity are chiefly inhabitants of larger and downstream waters. These phenomena are discussed in terms of faunal centers and barriers to dispersal.

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Mollusks of Alacran Reef, Campeche Bank, Mexico[1]

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Abstract

Photographic plates and descriptions are given for a collection of 90 species of gastropods and 40 species of pelecypods from Alacran Reef, Yucatan, Mexico, to aid in further study of the Campeche Bank.

Introduction

Alacran Reef, a shelf atoll situated about 70 miles north of Yucatan, Mexico, is the largest reef on the Campeche Bank, which is a carbonate shelf extending about 125 miles into the Gulf of Mexico.

The present paper describes mollusks collected on and in the immediate vicinity of Alacran Reef. The text is designed to facilitate identification of mollusks by investigators working on the Campeche Bank, where because of the similarity of the bank to carbonate deposits in the geologic column, and because of the relatively few carbonate areas in today's seas, we can expect many geological and biological investigations during the ensuing years.

In general the mollusks of Alacran Reef are similar to those of the West Indies and the Florida Keys. A similar molluscan assemblage was reported from Blanquilla Reef, which is in the Gulf of Mexico about 60 miles from Tampico, Mexico (Moore, 1958). The Alacran Reef molluscan assemblage differs considerably from that living along the coast of Texas. The present paper includes descriptions of 90 species of Gastropods and 40 species of Pelecypods.

The classification used in this paper is based principally on that of R. Tucker Abbott (*American Seashells*, 1955). In describing a shell, morphological characteristics of the shell considered taxonomically important by Abbott were stressed. Descriptions were based on shells from Alcaran Reef in the mollusk collection at the Institute of Marine Science. Previous papers concerning the Campeche Bank include those of Agassiz (1878, 1879), Rehder and Abbott (1951), Springer and Bullis (1956), and Kornicker, Bonet, Cann, and Hoskin (1959).

Systematic Descriptions

GASTROPODA

FISSURELLIDAE

Genus *Emarginula* Lamarck 1801

Emarginula phrixodes Dall. 6 mm in length. Translucent white. Narrow slit on anterior margin. Base oval. Finely cancellate sculpture of concentric cords, 20 to 20 radial ribs. Two specimens.

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Genus *Diodora* Gray 1821

Diodora minuta Lamarck. Plate 1, Fig. 3A, 3B. 7 to 9 mm. Thin, depressed. Base elliptical, raised slightly at center. Short front slope concave, back slope convex. Orifice narrow, trilobated. Exterior shiny; numerous finely beaded radial ribs. Color: white, many ribs entirely or partly black; internal callus bounded by black line. Six specimens.

Diodora listeri Orbigny. Plate 1, Fig. 1A, 1B. 19 to 38 mm. Shell large, heavy, conical, elevated. Base ovate. Orifice key-hole shaped. 38 to 40 strong, rounded radial ribs, alternately larger and smaller, crossed by 9 to 12 concentric threads to form small squares. Large scales or nodules produced where concentric threads and radial ribs cross. Color: dull white. Orifice blue-black. Nine specimens.

Genus *Lucapina* Sowerby 1835

Lucapina suffusa Reeve. Plate 1, Fig. 4A, 4B. 10 to 20 mm. Outline oblong. About 60 alternately large and small, radiating ribs, 9 to 13 raised concentric threads. Color: delicate mauve to pink. Orifice blue-black. Four specimens.

Lucapina philippiana Finlay. Plate 1, Fig. 2A, 2B. 10 to 18 mm. Very depressed, narrow. Base oblong, sides subparallel, front slope straight, about half the length of convex posterior slope. Orifice large, oblong. Finely sculptured; about 38 close, radiating, alternately large and small ribs starting at orifice; ribs beaded by 8 or 9 raised concentric threads. Color: dull white. Four specimens.

Genus *Hemitoma* Swainson 1840

Hemitoma emarginata de Blainville. Plate 1, Fig. 7A, 7B. 10 to 18 mm. Apex subcentral, recurved posteriorly. Strong reticulate sculpture; nodules formed where radial ribs and concentric ridges cross. Primary ribs 8 to 10. Anterior rib single, prominent, ending in small notch at margin. 1 to 3 secondary ribs between primary ribs. Anal groove extends from near apex to margin, ending in small notch. Color: white. Ten specimens.

ACMAEIDAE

Genus *Acmaea* Eschscholtz 1830

Acmaea jamaicensis Gmelin. Plate 1, Fig. 6A, 6B. 10 to 15 mm. Moderately high, thick; sides slightly convex. 15 to 20 rounded, white radial ribs on tan background. Interior white, with tan, thickened central callus. Five specimens.

Acmaea pustulata pulcherrima Guilding. Plate 1, Fig. 5A, 5B. 10 to 12 mm. Outline oval. Moderately flat, apex sharp. Shell thin, light pink in color, flecked with red. Six specimens.

TROCHIDAE

Genus *Calliostoma* Swainson 1840

Calliostoma zonamestum A. Adams. Plate 2, Fig. 7. 23 mm in diameter, 15 mm high. Sides of whorls flat. Periphery sharp, base flat. Dark brown line between each of 10 beaded, spiral threads. Umbilicus white, deep, smooth-sided. One specimen.

Calliostoma jujubinum Gmelin. Plate 2, Fig. 6. 24 mm in diameter. Distinguished by swollen, rounded periphery of each whorl which in spire is located just above suture. Color: light tan with splotches of brown. Umbilicus white, deep, narrow, smooth-sided, bordered by beaded spiral thread. Two specimens.

Calliostoma sp. Plate 4, Fig. 18. 11 mm in length, not quite so high. Imperforate. Sculpture of numerous spiral, beaded threads. Cream color, apical whorls with dark spiral cord below suture. Three specimens.

Genus *Tegula* Lesson 1832

Tegula fasciata Born. 4 to 8 mm in diameter. 4 to 6 flat whorls. Color: white or cream; top of whorls splotched with deep pink to brown. Numerous fine, spiral threads. Umbilicus deep, round, smooth. Two teeth at base of columella. Twelve specimens.

Turbinidae

Genus *Cyclostrema* Marryat 1818

Cyclostrema cancellatum Marryat. Plate 3, Fig. 21. 3 to 6 mm in diameter. 2 to 3 flat-topped whorls. Color: frosted white. Sculpture of 14 rounded axial ribs which encircle entire whorl. Nodules formed at intersection of axial ribs and smaller spiral cords. Fourth, fifth and sixth spiral cords situated respectively at top, middle and bottom of periphery of whorl. Umbilicus wide, deep. Aperture circular and thickened. Sixteen specimens collected from beach sand.

Genus *Arene* H. and A. Adams 1854

Arene cf. *cruentata* Mühlfeld. Plate 4, Fig. 15. 6 to 8 mm in diameter, half as high. Color: white with small red dots on top of 4 to 5 angular whorls. Top of periphery bearing series of horizontal, open, triangular spines; minor row of smaller spines at middle of periphery, every third spine pink to red. Strong, beaded, spiral cord at base of periphery. Aperture circular. Umbilicus round, deep; bordered by 3 spiral, beaded cords. Ten specimens collected from beach sand.

Genus *Turbo* Linnaeus 1758

Turbo cailletii Fischer and Bernard. Plate 2, Fig. 11, 12. Slightly more than 25 mm. Color: cream with dark brown, flame-like patches. Sculpture of irregular spiral cords; coarse on upper half of body whorl, finer and more numerous on base of shell. Lower lip projects downward. Aperture white. Callus on columella, heavy. Two specimens.

Genus *Astraea* Röding 1798

Astraea longispina Lamarck. Plate 5, Fig. 18. 44 to 63 mm in diameter; low spire, base almost flat. Periphery of whorls with strong, flat, triangular spines. Aperture lustrous. Operculum calcareous. Six specimens.

Astraea americana Gmelin. Plate 2, Fig. 14. 25 to 38 mm in length, not quite so wide. Color: cream. Spire elevated, sides flat. Sculpture of oblique radial folds; 5 to 8 fine spiral cords on base of shell. Operculum calcareous, thick, convex. Eight specimens.

Astraea caelata Gmelin. Plate 5, Fig. 17. 25 to 50 mm in diameter, not quite so high. Color: cream with splotches of pinkish-brown. 3 to 5 uneven spiral rows of hollow, scale-like spines on upper body whorl; base with 4 to 6 strong spiral cords. Entire body whorl with numerous oblique, finely fimbriated, radial lamellae. Operculum thick, convex, papillose. Seven specimens.

Phasianellidae

Genus *Tricolia* Risso 1826

Tricolia cf. *thalassicola* Robertson. Plate 3, Fig. 19. About 4 mm. 6 rounded whorls. White with minute dots of greenish yellow; 7 patches of bright pink dots spirally arranged below suture and at periphery. Numerous beach specimens.

Neritidae

Genus *Nerita* Linnaeus 1758

Nerita peloronta Linnaeus. Plate 2, Fig. 8. 16 to 18 mm. Color: grayish-yellow with streaks and patches of purple or black. Distinguished by red stain on parietal area which bears 1 to 2 white teeth. Sculpture of flat spiral ridges which become obscure on last half of body whorl. Operculum pink on underside; outerside smooth, orange colored on lower half, gray green, papillose on upper half. Four specimens.

Nerita versicolor Gmelin. Plate 2, Fig. 10. 12 to 21 mm. Color: grayish-white with irregular zigzag rows of black and purplish-pink spots. Sculpture of strong, rounded, spiral ridges which extend to edge of outer lip. Parietal area yellowish-white with 4 teeth; middle 2 larger than outer ones. Operculum grayish-brown, concave, papillose on lower half. Ten specimens.

Nerita tessellata Gmelin. Plate 2, Fig. 9. 10 to 18 mm. Color: chalky white with squarish black spots which form irregular checkered pattern. Apex pale yellow. Outer lip blue-white with black spots. Columellar lip with 2 weak teeth in middle; teeth inconspicuous in immature specimens. This species characterized by black operculum which is papillose, slightly convex. Ten specimens.

Genus *Neritina* Lamarck 1816

Neritina virginea Linnaeus. Pl. 3, Fig. 7. 8 to 12 mm. Smooth, glossy. Color: olive green with varied patterns of grayish-white; some spirally banded, others spotted or mottled. Columellar area smooth, white, convex with 6 to 12 small, irregular teeth. Operculum black. Ten specimens.

Genus *Smaragdia* Issel 1869

Smaragdia viridis Linnaeus. Pl. 4, Fig. 13. 3 to 7 mm. Pale green in color with short, white, radial streaks. Columellar lip white with several small, irregular teeth. Twenty-four specimens collected from beach sand.

Littorinidae

Genus *Littorina* Ferussac 1821

Littorina ziczac Gmelin. Plate 3, Fig. 6, 8. 8 to 18 mm. Shell bluish-white with numerous zigzag, oblique lines of dark brown. Aperture purplish-brown. Well defined keel near

base of body whorl. Operculum dark brown. Six specimens. (Abbott gives the length of females of this species about 1 inch, higher than wide, smoothish; male shells about ½ inch, as high as wide with strong spiral grooves.)

Genus *Nodilittorina* Martens 1897

Nodilittorina tuberculata Menke. Plate 3, Fig. 4. 10 to 15 mm. 7 to 8 whorls. Shell rounded at base. Nuclear whorls have fine, spiral threads. Succeeding whorls bear 2 or 3 spiral rows of small, pointed nodules. Largest nodules on second and third row. 7 rows of nodules on body whorl. Columella flattened and dished out. Outer lip projects below columella. Color: brownish-gray, nodules whitish; columella and aperture dark brown. Operculum paucispiral, dark brown, chitinous. Seven specimens.

RISSOIDAE

Genus *Rissoina* Orbigny 1840

Rissoina chesneli Michaud. Plate 3, Fig. 16. 3 mm. 5 glossy white whorls with 12 radial ribs.

Rissoina multicostata C. B. Adams. Plate 3, Fig. 14. 4 to 5 mm. Shell white with 5 to 7 whorls. 21 axial ribs, weaker spiral cords. Ribs disappear on base; spiral threads strongest on base.

Rissoina cancellata Philippi. Plate 3, Fig. 13. 5 to 7 mm. White, 6 to 8 whorls. Sculpture strongly cancellate. Depressed interspaces large, square.

Rissoina browniana Orbigny. 4 to 5 mm. Smooth, glossy white.

VERMETIDAE

Genus *Petaloconchus* H. C. Lea 1843

Petaloconchus cf. *nigricans* Dall. Plate 2, Fig. 18. Closely packed, irregular mass, each tube about 2 mm in diameter. Color: dirty gray. Longitudinal sculpture of finely beaded cords.

SILIQUARIIDAE

Genus *Vermicularia* Lamarck 1799

Vermicularia knorri Deshayes. Plate 2, Fig. 16, 17. 19 to 50 mm. Evenly coiled portions translucent white, subsequent whorls brown. Six specimens.

CAECIDAE

Genus *Caecum* Fleming 1817

Caecum cooperi S. Smith. Plate 3, Fig. 22. 3.5 mm. Cream to tan in color, glossy. Sculpture of about 15 longitudinal ribs; strong, raised axial rings near aperture form cancellated sculpture on anterior end. Pointed prong on apical plug.

Caecum floridanum Stimpson. Plate 3, Fig. 23. 2 to 4 mm. Dull white. 20 to 30 strong axial rings, the last 3 or 4 much enlarged. Slightly recessed apical plug with pointed prong.

base of body whorl. Operculum dark brown. Six specimens. (Abbott gives the length of females of this species about 1 inch, higher than wide, smoothish; male shells about ½ inch, as high as wide with strong spiral grooves.)

Genus *Nodilittorina* Martens 1897

Nodilittorina tuberculata Menke. Plate 3, Fig. 4. 10 to 15 mm. 7 to 8 whorls. Shell rounded at base. Nuclear whorls have fine, spiral threads. Succeeding whorls bear 2 or 3 spiral rows of small, pointed nodules. Largest nodules on second and third row. 7 rows of nodules on body whorl. Columella flattened and dished out. Outer lip projects below columella. Color: brownish-gray, nodules whitish; columella and aperture dark brown. Operculum paucispiral, dark brown, chitinous. Seven specimens.

RISSOIDAE

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Rissoina chesneli Michaud. Plate 3, Fig. 16. 3 mm. 5 glossy white whorls with 12 radial ribs.

Rissoina multicostata C. B. Adams. Plate 3, Fig. 14. 4 to 5 mm. Shell white with 5 to 7 whorls. 21 axial ribs, weaker spiral cords. Ribs disappear on base; spiral threads strongest on base.

Rissoina cancellata Philippi. Plate 3, Fig. 13. 5 to 7 mm. White, 6 to 8 whorls. Sculpture strongly cancellate. Depressed interspaces large, square.

Rissoina browniana Orbigny. 4 to 5 mm. Smooth, glossy white.

VERMETIDAE

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SILIQUARIIDAE

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Caecum floridanum Stimpson. Plate 3, Fig. 23. 2 to 4 mm. Dull white. 20 to 30 strong axial rings, the last 3 or 4 much enlarged. Slightly recessed apical plug with pointed prong.

Caecum nebulosum Rehder. Plate 3, Fig. 24. Slightly more than 2 mm. Translucent white with opaque mottling. Not swollen at center. Aperture oblique. Apical plug with weak projection on highest side.

Modulidae

Genus *Modulus* Gray 1842

Modulus modulus Linnaeus. Plate 4, Fig. 16. 5 to 7 mm in diameter. Shell umbilicate. Periphery of body whorl angulate. Sculpture variable; top of whorls with axial ribs or only spiral threads. Base with 4 to 6 spiral cords. Tooth at base of columella. Color: white with brown spots on spiral cords. Twenty-four specimens.

Potamididae

Genus *Batillaria* Benson 1842

Batillaria minima Gmelin. Plate 4, Fig. 14. 3 to 9 mm. Color: rusty to blackish-brown. Apex eroded, chalky. Irregular spiral cords, finely nodulose. Aperture dark brown. Short siphonal canal twisted to left. Operculum multispiral. Twenty-four specimens.

Cerithiidae

Genus *Cerithium* Bruguiere 1789

Cerithium literatum Born. Plate 2, Fig. 2. 10 to 30 mm in length, half as wide. Color: white with spiral rows of dark brown dashes. Spiral row of 8 to 12 sharp nodules just below suture. Eight specimens.

Cerithium variabile C. B. Adams. Plate 4, Fig. 3. 12 to 15 mm. Color: white with brown mottlings. Sculpture of 3 irregularly beaded, spiral cords. 1 to 2 former varices on each whorl. Three specimens.

Cerithium algicola C. B. Adams. Plate 3, Fig. 10. 20 to 22 mm. Color: white with brown mottlings. Each whorl has middle spiral row of 9 to 12 beads, large, sharply pointed. Three specimens.

Cerithium eburneum Bruguiere. Plate 4, Fig. 20, 20 to 24 mm. Color: white with tan splotches. 4 to 5 spiral rows of 18 to 22 beads on each whorl, center row only slightly larger; beads rounded, not sharp or pointed. Former varies on each whorl. Two specimens.

Genus *Seila* A. Adams 1861

Seila adamsi H. C. Lea. Plate 3, Fig. 12. I beachworn specimen 8 mm. Color: yellow. Slender, flat-sided whorls. Sculpture of close, smooth, squarish, spiral cords.

Genus *Alaba* H. and A. Adams 1853

Alaba sp. Plate 3, Fig. 11. 7 mm. 9 convex whorls; nuclear whorls broken. Sculpture of spiral grooves, strongest on lower half of each whorl. Several former varices. Shell translucent white.

Caecum nebulosum Rehder. Plate 3, Fig. 24. Slightly more than 2 mm. Translucent white with opaque mottling. Not swollen at center. Aperture oblique. Apical plug with weak projection on highest side.

Modulidae

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Modulus modulus Linnaeus. Plate 4, Fig. 16. 5 to 7 mm in diameter. Shell umbilicate. Periphery of body whorl angulate. Sculpture variable; top of whorls with axial ribs or only spiral threads. Base with 4 to 6 spiral cords. Tooth at base of columella. Color: white with brown spots on spiral cords. Twenty-four specimens.

Potamididae

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Cerithium algicola C. B. Adams. Plate 3, Fig. 10. 20 to 22 mm. Color: white with brown mottlings. Each whorl has middle spiral row of 9 to 12 beads, large, sharply pointed. Three specimens.

Cerithium eburneum Bruguiere. Plate 4, Fig. 20, 20 to 24 mm. Color: white with tan splotches. 4 to 5 spiral rows of 18 to 22 beads on each whorl, center row only slightly larger; beads rounded, not sharp or pointed. Former varies on each whorl. Two specimens.

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Alaba sp. Plate 3, Fig. 11. 7 mm. 9 convex whorls; nuclear whorls broken. Sculpture of spiral grooves, strongest on lower half of each whorl. Several former varices. Shell translucent white.

TRIPHORIDAE

Genus *Triphora* Blainville 1828

Triphora decorata C. B. Adams. Plate 4, Figure 4. 2 beachworn specimens 10, 12 mm. Sinistral, elongated, flat-sided. 3 evenly beaded, spiral cords on each whorl. White with irregular, radial streaks of brown.

EPITONIIDAE

Genus *Epitonium* Röding 1798

Epitonium sp. Plate 4, Fig. 19. 12 mm. Glossy white. Axial costae 12, high, thin, sharp.

EULIMIDAE

Genus *Balcis* Leach 1847

Balcis sp. Plate 3, Fig. 17. 6 mm. Glossy white. Conic, body whorl rounded. Outer lip thin, sharp.

HIPPONICIDAE

Genus *Cheilea* Modeer 1793

Cheilea equestris Linnaeus. Plate 1, Fig. 8A, 8B. 5 to 12 mm. Cap-shaped; frosted white. Fragile, internal, tube-like structure, anterior third cut away, attached slightly off center. Exterior with sculpture of delicate, concentric, fimbriated lamellae. Four specimens.

Genus *Hipponix* Defrance 1819

Hipponix antiquatus Linnaeus. Plate 1, Fig. 9A, 9B. 5 to 12 mm in diameter. Cap-shaped. Spire deflected back and downward. Exterior appears concentrically lamellated. Muscle scar horse-shoe shaped. Color: dull white. Ten specimens.

CALYPTRAEIDAE

Genus *Crepidula* Lamarck 1799

Crepidula plana Say. 20 mm. Oblong, thin, very flat. Upper side dull white, underside glossy. Two specimens.

STROMBIDAE

Genus *Strombus* Linnaeus 1758

Strombus gigas Linnaeus. Pl. 5, Fig. 1, 2. 63 to 173 mm. Color: dark cream or tan externally, smaller specimens mottled with brown; aperture pink. Large, fairly sharp spines on shoulder of whorls. Outer lip thin; shell relatively light in weight. The flaring lip, characteristic of this species, is undeveloped. Fourteen immature specimens.

Strombus costatus Gmelin. Plate 5, Fig. 6, 9. 100 to 150 mm. Shell heavy, with low, blunt spines; the last 3 or 4 on body whorl much enlarged. Color varies from cream to

burnt orange externally; aperture china-white. Parietal wall and thick outer lip highly glazed with greenish-silver enamel. Six specimens.

Strombus raninus Gmelin. Plate 5, Fig. 5, 10. 88 mm. Grayish-white in color with chocolate brown mottling. Aperture salmon pink. Parietal wall and outer lip covered with an aluminium-like glaze. Blunt spines on shoulder of body whorl, last 2 conspicuously larger. Numerous spiral lines on last two-thirds of body whorl. Thick outer lip extends above shoulder of body whorl into a short blunt wing which is not as high as spire of shell. Two specimens.

Eratoidae

Genus *Trivia* Broderip 1837

Trivia suffusa Gray. Plate 4, Fig. 17. 6 to 12 mm. Elongate-globular. Color: pale pink with 3 brown splotches on each side of dorsal groove. 12 to 20 finely beaded riblets cross pink outer lip. Eight specimens.

Trivia quadripunctata Gray. 6 to 8 mm. Elongate-globular. Color: bright pink with 2 to 3 small brown spots along short dorsal groove. 19 to 21 smooth ribs cross outer lip.

Ovulidae

Genus *Cyphoma* Röding 1798

Cyphoma gibbosum Linnaeus. Plate 2, Fig. 5A, 5B. 30 and 35 mm. Porcelaneous. Color: pinkish-buff except for whitish rectangle on back; aperture white. Two specimens.

Naticidae

Genus *Polinices* Montfort 1810

Polinices lacteus Guilding. 8 to 20 mm in height. Six specimens, all beach worn. Ovate. Glossy, milk-white. Umbilicus partially closed by heavy parietal callus.

Genus *Sinum* Röding 1798

Sinum perspectivum Say. Plate 3, Fig. 20. One specimen, 27 mm in diameter. Auriform; aperture widely flared. Color: white, interior glossy. Sculpture of wavy spiral threads crossed by fine growth lines.

Genus *Natica* Scopoli 1777

Natica canrena Linnaeus. Plate 5, Fig. 15. One specimen. 38 mm. Color: ivory with brown, wavy, axial lines. 4 spiral rows of brown, arrow-shaped marks. Shell smooth except for weak wrinkles near suture. White callus partially fills deep umbilicus.

Natica livida Pfeiffer. 12 mm. Shell moderately thin; glossy smooth. Color: light gray with 2 weak spiral bands of tan. Umbilicus partially closed by light brown callus. One specimen.

Cassididae

Genus *Cassis* Scopoli 1777

Cassis madagascariensis spinella Clench. One beach worn specimen, 213 mm. Color: cream. 3 spiral rows of small, rounded nodules on body whorl; top row largest.

Parietal area blackish-brown between ridge-like teeth. Light brown inside aperture. Outer lip color of body whorl, brown between teeth.

Cymatiidae

Genus *Cymatium* Röding 1798

Cymatium pileare Linnaeus. Plate 5, Fig. 19. One beachworn specimen, 50 mm. Sculpture of irregular, squarish, weakly beaded, spiral cords. Color: white with bands of light brown; outer lip tan between lighter colored teeth which are grouped in pairs. Parietal wall brown between numerous, irregular, white folds.

Cymatium caribbaeum Clench and Turner. Plate 2, Fig. 15. One worn specimen, 44 mm. Body whorl globular, shoulders angulate; previous whorls flat-sided. Apical whorls cancellate; strongly beaded spiral cords on body whorl. 1 former varix. Thick outer lip with 7 large, single, white teeth. Color: light tan.

Cymatium gemmatum Reeve. Plate 2, Fig. 1. One specimen, 31 mm. Shell white or cream, covered with thin straw colored periostracum, smooth over most of shell but producing fringed blades on axial ribs. Whorls squarish at shoulders. Spiral sculpture of finely beaded cords. Body whorl with 6 brown nodules at periphery. 1 varix. Aperture elongate-oval, pale apricot within; large columellar tooth at upper edge. Thickened outer lip with 12 teeth grouped in pairs.

Cymatium nicobaricum Röding. 60 mm; nucleus broken. Spire extended, whorls shouldered. Coarse sculpture of 6 irregular, nodulose, spiral ribs interspaced with 2 smaller cords. Variable axial folds between varices. Color: ashen gray; aperture bright orange, with 7, single, ridge-like, white teeth. One specimen.

Tonnidae

Genus *Tonna* Brunnich 1772

Tonna maculosa Dillwyn. Plate 5, Fig. 13. One specimen 69 mm. Shell thin. Color: cream mottled with light brown. Nuclear whorls golden brown, smooth. Numerous broad, flat, spiral cords. This species is longer than wide.

Tonna galea Linnaeus. Plate 5, Fig. 11, 16. 50 to 75 mm. Globular, fairly thin. Nuclear whorls smooth, dark brown. 18 to 21 broad, flat, spiral ribs; fine spiral cord between each rib on upper half of body whorl. Fresh specimens cream to tan in color, some slightly mottled with brown; older shells bleached white. Eighteen specimens.

Muricidae

Genus *Murex* Linnaeus 1758

Murex pomum Gmelin. 63 mm. One beach worn specimen. Shell thick, dirty white. 2 short axial folds between each of 3 varices. Dark brown spot at upper edge of parietal area. Outer lip crenulate, with 3 evenly spaced brown spots.

Genus *Drupa* Röding 1798

Drupa nodulosa C. B. Adams. Plate 3, Fig. 5. 10 to 18 mm. Elongate. Sculpture of round, black nodules, axially aligned. Aperture dark purple. Thick outer lip with 4 white teeth. Twelve specimens.

Genus *Thais* Röding 1798

Thais deltoidea Lamarck. Plate 2, Fig. 13. 31 to 44 mm. Shells grayish-white. Spiral row of large, blunt spines at shoulder of body whorl. Some specimens show second row of much smaller spines below first. Aperture china-white; parietal area tinted lavender. Nine specimens.

COLUMBELLIDAE

Genus *Columbella* Lamarck 1799

Columbella mercatoria Linnaeus. Pl. 4, Fig. 5. 8 to 15 mm. Color: white, with broken, spiral streaks of brown. Sculpture of numerous spiral grooves. Aperture long, narrow. 10 to 12 white teeth on outer lip which is thickened, particularly in the middle. Fifty specimens.

Genus *Nitidella* Swainson 1840

Nitidella nitidula Sowerby. Plate 4, Fig. 7. One specimen. 10 mm. Color: cream with orange splotches. 7 sloping whorls, no shoulders. Spire sharply pointed. Surface of shell smoothish, faint spiral threads on lower one-fourth of last whorl. Outer lip only slightly thickened.

Genus *Anachis* H. and A. Adams 1853

Anachis pulchella Sowerby. Plate 4, Fig. 6. 8 to 10 mm. Translucent, lightly mottled with yellow. Numerous low, axial ribs crossed by spiral striae. Ribs strongest on upper whorls. Only beach specimens collected.

BUCCINIDAE

Genus *Bailya* M. Smith 1944

Bailya intricata Dall. Plate 4, Fig. 1. One beach specimen. 12 mm. Frosted white, with 2 faint brownish, spiral bands on body whorl. 6 shouldered whorls; nuclear whorls broken. Surface cancellate; body whorl with 12 axial riblets crossed by 8 spiral cords with smaller threads between; beaded at intersection. Outer lip with rounded varix.

Genus *Cantharus* Röding 1798

Cantharus tinctus Conrad. 23 to 25 mm. Sloping whorls. Small posterior canal. Outer lip thickened. Sculpture of 10 axial folds crossed by numerous spiral threads. Color: grayish-brown with dark blue splotches on glazed parietal wall. Two specimens.

MELONGENIDAE

Genus *Cantharus* Röding 1798

Busycon contrarium Conrad. Plate 5, Fig. 12. 106 to 193 mm. Sinistral. Shell relatively heavy. Spire low, whorls shouldered. Spiral row of spines on shoulder, largest on body whorl. Surface covered with wavy, spiral threads. Color: cream to dark tan

with white spiral band at center of body whorl. Color inside aperture varies from deep cream to orange. Eight specimens.

Busycon spiratum Lamarck. Plate 5, Fig. 7. 31 to 113 mm. Shell thin, spire flattened. Shoulders slightly keeled. Suture marked by deep, narrow channel. Sculpture of very fine, spiral threads. White with 2 to 3 spiral rows of brown splotches. Fifteen specimens.

Nassariidae

Genus *Nassarius* Dumeril 1806

Nassarius ambiguus Pultney. Plate 4, Fig. 2. 6 to 12 mm. Color: white with 2 narrow bands of light brown, obscure in these beach specimens. Relatively light shelled. Whorls shouldered. 10 to 12 axial ribs on each whorl; numerous small, spiral threads. Eight specimens.

Fasciolariidae

Genus *Leucozonia* Gray 1847

Leucozonia nassa Gmelin. Plate 5, Fig. 14. 31 to 44 mm. Shell thick; shoulders well-rounded, marked by obscure nodules which are more prominent on penultimate whorl. 4 columellar folds. Color: dark brown; aperture dark cream within. Six specimens.

Genus *Fasciolaria* Lamarck 1799

Fasciolaria tulipa Linnaeus. Plate 5, Fig. 4, 8. 56 to 131 mm. Characterized by 2 or 3 spiral grooves just below suture. Gray with broken spiral lines, blotches of blackish-brown. Inside aperture glossy cream color. Six specimens.

Genus *Pleuroploca* P. Fischer 1884

Pleuroploca gigantea Kiener. Two beach worn specimens, each about 250 mm. Nuclear whorls broken. Yellowish-white. Shouldered whorls with 8 large nodules on shoulder of body whorl. Coarse, irregular, spiral ribs.

Xancidae

Genus *Xancus* Röding 1798

Xancus angulatus Solander. Plate 5, Fig. 3. One specimen, 113 mm. Shell thick, heavy, cream colored, interior tinged with pale pink. 3 strong, widely spaced columellar folds. Spiral ridge inside aperture about middle of outer lip.

Olividae

Genus *Olivella* Swainson 1831

Olivella nivea Gmelin. Plate 4, Fig. 9. 5 to 14 mm. Elongate. 5 to 6 whorls. Apex pointed. Shell glossy white; nucleus tan in fresh specimens. Numerous columella folds.

MITRIDAE

Genus *Pusia* Swainson 1840

Pusia gemmata Sowerby. Plate 3, Fig. 15. 5 to 6 mm in length. Beach specimens. Tan, with white spiral band bearing 11 to 13 nodules on each whorl.

MARGINELLIDAE

Genus *Prunum* Herrmannsen 1852

Prunum labiatum Valenciennes. Plate 2, Fig. 4. Porcelaneous. Outer lip thickened, dull orange, tiny teeth on inner edge. Body whorl grayish-white with 3 cloudy, spiral bands of dull lavender. 25 to 30 mm. Five specimens.

Prunum guttatum Dillwyn. Plate 3, Fig. 1. One specimen, 15 mm. Body whorl grayish-white, irregularly spotted with opaque white dots. Stout outer lip smooth. Color: white, with three brown spots on lower half. 4 strong, columellar folds.

Genus *Hyalina* Schumacher 1817

Hyalina avena Valenciennes. Plate 4, Fig. 8. 9 to 11 mm. Ivory colored with several obscure bands of light tan. Shell slender, spire short. Outer lip rolled in, smooth. Aperture narrow above, wide below. Four slanting columellar folds. Four specimens collected from beach sand.

Genus *Persicula* Schumacher 1817

Persicula sp. Plate 4, Fig. 11. 5 to 6 mm. Apical area slightly concave, sealed over by thin callus. 20 to 25 tiny teeth inside outer lip. 5 to 6 columellar folds; first 2 folds very weak. Shell glossy white with several spiral rows of brown arrow-shaped marks. Four specimens.

CONIDAE

Genus *Conus* Linnaeus 1758

Conus spurius atlanticus Clench. One specimen, 59 mm. Spire slightly elevated in the center. Shell smooth, white with spiral rows of squarish orange spots and blotches. Aperture white.

Conus mus Hwass. Plate 2, Fig. 3. One specimen, 31 mm. Spire moderately elevated. Color: mottled grayish-brown. Low, irregular, white knobs on shoulder. 2 wide, spiral, brown bands inside aperture. Periostracum thick, velvety, dull brown.

TURRIDAE

Genus *Glyphoturris* Woodring 1928

Glyphoturris quadrata rugirima Dall. About 6 mm. Frosted white. Sculpture of high axial ribs, 8 on body whorl. Ribs sharply angulated at center of each whorl and crossed by faintly beaded, spiral threads. One specimen.

Bullidae

Genus *Bulla* Linnaeus 1758

Bulla sp. Plate 3, Fig. 2. 8 to 14 mm. Color: white to tan with brown mottling. Callus white. Spiral grooves well-marked toward base of shell and within apical perforation. Fifteen specimens.

Atyidae

Genus *Haminoea* Turton and Kingston 1830

Haminoea succinea Conrad. Plate 4, Fig. 12. One specimen, 7 mm. Translucent white. Apertural lip rises on right side of perforation, not angled. Sides of whorls flattish. Numerous spiral grooves.

Genus *Atys* Montfort 1810

Atys caribaea Orbigny. Plate 3, Fig. 3. 5 to 6 mm. Elongate-oval. Translucent milk-white. Central part of shell smooth; about 12 very fine, incised spiral lines at both ends. Spire concealed. Aperture long, narrow with outer lip rising well above top of shell and projecting below columella. Six specimens collected from beach.

Atys sandersoni Dall. Plate 4, Fig. 10. 5 to 8 mm. Similar to *A. caribaea* but with flatter sides, more numerous, finer, spiral lines at each end. Ten specimens.

Retusidae

Genus *Retusa* Brown 1827

Retusa canaliculata Say. 4 to 5 mm. Oblong, flat-sided, smooth, glossy white. Tiny pimple-like nucleus. Aperture narrow at posterior end, wider anteriorly. Outer lip thin. Six specimens.

Pyramidellidae

Genus *Odostomia* Fleming 1817

Odostomia sp. Plate 3, Fig. 18. 2 mm. Frosted white. Sculpture of strong, squarish, faintly beaded spiral cords. Two specimens.

Pelecypoda

Arcidae

Genus *Arca* Linnaeus 1758

Arca zebra Swainson. Plate 6, Fig. 8A, 8B. 44 to 62 mm in length, about half as high. Color: light brown with zebra-stripes of dark brown. Radial ribs only. Relatively small bysal gap. Beaks widely separated, with broad, flat area between. Two specimens.

Arca umbonata Lamarck. Plate 6, Fig. 7A, 7B. 37 to 53 mm, box-like, elongate. Shell tan to brown mottled with darker brown. Interior lighter in color. Beaks widely

separated with concave area between. Numerous irregular, beaded radial ribs. Large bysal gap. Periostracum very heavy on live specimens. Seven specimens.

Genus *Barbatia* Gray 1847

Barbatia domingensis Lamarck. Plate 9, Fig. 7A, 7B. 20 mm. Color: grayish-white. Shell moderately inflated. Reticulated sculpture. Inner margins denticulate. One specimen.

Barbatia cancellaria Lamarck. Plate 8, Fig. 12A, 12B. 15 to 35 mm. Flattish, fairly thin. Sculpture of numerous, well beaded, axial cords. Dark purplish-brown in color. Ten specimens.

Genus *Arcopsis* von Koenen 1885

Arcopsis adamsi E. A. Smith. Plate 9, Fig. 8. One specimen, 6 mm. Oblong, inflated. Color: white. Cancellate sculpture. Small brown diamond-shaped ligament between umbones.

GLYCYMERIDAE

Genus *Glycymeris* Da Costa 1778

Glycymeris pectinata Gmelin. Plate 9, Fig. 6A, 6B. One beach worn specimen, 20 mm. Sculpture of 22 smooth, radial ribs. Color: gray-white with concentric line of brown midway of valves; flecks of brown scattered over shell.

MYTILIDAE

Genus *Modiolus* Lamarck 1799

Modiolus americanus Leach. Plate 7, Fig. 7A, 7B. 2½ to 3½ inches. Smooth, except for growth lines. Shell white, flushed with rose or purple. Interior iridescent with external color visible. Fresh specimens covered with dark brown periostracum, glossy on anterior area, beard-like at posterior margin. Ten specimens.

Genus *Brachidontes* Swainson 1840

Brachidontes citrinus Röding. Plate 8, Fig. 13. 31 mm, narrow. Color white with yellow periostracum. Sculpture of numerous, fine, radial, riblets: 1 specimen.

Genus *Lithophaga* Röding 1798

Lithophaga nigra Orbigny. Plate 7, Fig. 8A, 8B. 40 to 53 mm, cylindrical. Brownish-black outside, iridescent blue-white inside. Weak vertical lines on lower anterior third of each valve, remainder of shell smooth. Four specimens.

ISOGNOMONIDAE

Genus *Isognomon* Solander 1786

Isognomon alatus Gmelin. Plate 9, Fig. 11A, 11B. 13 to 32 mm. Roughly oval in outline. Right valve flat or slightly concave, left valve convex. Hinge with 4 to 6 oblong

sockets. Exterior color varies from dull white to purple; interior nacreous. Six specimens.

Isognomon radiatus Anton. 82 mm. Elongate. Exterior coarsely lamellated; interior nacreous except on ventral margins. Right valve concave, left valve convex. Hinge short, 5 small oblong sockets. Color: yellowish-gray with purplish radial streaks on convex valve. One specimen.

Isognomon cf. *bicolor* C. B. Adams. Plate 9, Fig. 10A, 10B. 15 mm in height, 10 mm wide. Valves slightly inflated. Exterior smooth except for irregular growth lines. Color: dull gray. Hinge has 7 oblong sockets. Interior of both valves with squarish, saucer-like depression, located in upper half; outlined by raised, fairly sharp rim. Depressed area and rim opalescent; wide ventral margin dark purple. One specimen.

Pteriidae

Genus *Pinctada* Röding 1798

Pinctada radiata Leach. Plate 6, Fig. 6A, 6B, 9. 37 to 56 mm. Thin shelled, slightly inflated. Narrow ligament, center third of hinge line. Exterior rough with weak, flaky lamellations; interior nacreous. Color varies from dull white to pale brown, mottled or rayed with purple. Ten specimens.

Pinnidae

Genus *Pinna* Linnaeus 1758

Pinna carnea Gmelin. 88 to 288 mm. Color: flesh pink to deep burnt orange. Shell thin, inflated. Posterior end rounded, gaping. About 10 radial ridges with and without large open spines. Six specimens.

Pectinidae

Genus *Lyropecten* Conrad 1862

Lyropecten antillarum Recluz. Plate 8, Fig. 7A, 7B. 20 mm in length, about as wide. Color: white. Shell thin, flat, with 10 smooth, rounded, radial ribs. Two specimens.

Genus *Chlamys* Röding 1798

Chlamys imbricata Gmelin. Plate 8, Fig. 2, 5. 21 to 40 mm in height, not as wide. Upper valve nearly flat, lower valve convex. 9 to 10 radial ribs, each with evenly spaced, hollow knobs; where broken, these knobs appear as cup-shaped scales. Color: white or pinkish with small red spots; interior yellowish, some specimens white. Ten specimens.

Spondylidae

Genus *Spondylus* Linnaeus 1758

Spondylus americanus Hermann. Plate 8, Fig. 9A, 9B. 1 upper valve, 25 mm in diameter; thin. Exterior purplish-red, interior iridescent. Numerous closely set spines, nearly erect, varying from flat to needle-like in shape.

Limidae

Genus *Lima* Bruguiere 1797

Lima scabra Born. Plate 7, Fig. 4A, 4B. 50 to 75 mm in height. Elongate-oval in outline. Color: white or yellowish. Sculpture of radial ribs bearing short, irregularly spaced, shingle-like scales. Long bysal gap. Three specimens.

Lima lima Linnaeus. Plate 8, Fig. 8A, 8B. 10 to 34 mm in height. Color: pure white. Anterior ear much larger than posterior one, giving apex slightly pointed appearance. Sculpture of about 28, even, radial ribs bearing numerous sharp, erect scales. Twelve specimens.

Lima pellucida C. B. Adams. 25 mm. Shell fragile; translucent white. Gaping anteriorly and posteriorly. Sculpture of numerous, fine, radial threads. Beaks smooth, centrally located. One specimen.

Ostreidae

Genus *Ostrea* Linnaeus 1758

Ostrea frons Linnaeus. Plate 6, Fig. 4A, 4B, 4C. One articulated specimen, about 50 mm in length, half as wide; attached to twig by finger-like processes. Upper valve with broad, longitudinal mid-rib. Margins sharply plicate. Minute pimples on inner margin of upper valve. Exterior purple, interior iridescent.

Carditidae

Genus *Venericardia* Conrad 1867

Venericardia sp. Plate 9, Fig. 9A, 9B. 3 mm in length, about as high. Shell thick with 17 to 18 strong, evenly beaded, radial ribs. Beaks close together and turned forward. Color varies from white to pink with faint mottling. Six specimens.

Lucinidae

Genus *Lucina* Bruguiere 1797

Lucina pensylvanica Linnaeus. Plate 8, Fig. 6A, 6B. 18 to 37 mm. Color: glossy white. Thin, straw-colored periostracum. Shell relatively thick, ovate, well inflated. Fresh specimens show numerous fine, concentric ridges. Strong posterior groove from beaks to ventral margin. Five specimens.

Genus *Codakia* Scopoli 1777

Codakia cf. *orbiculata* Montagu. Plate 9, Fig. 1A, 1B, 3A, 3B. 8 to 11 mm. White. Obliquely rounded in outline. Large, elongate lunule. Numerous radial ribs extend to beaks; crossed by fine, concentric threads and coarser growth lines. Ten specimens.

Codakia orbicularis Linnaeus. Plate 6, Fig. 2A, 2B. 25 to 75 mm. Orbicular in outline. Mature specimens moderately thick, heavy. Coarse, divaricate ribs are crossed by fine, concentric threads giving ribs beaded appearance. Beaks smooth, except for microscopic radial lines, yellowish. Lunule small, heart-shaped, nearly all in right

valve. Exterior white, interior white to pale yellow; rose tinted interior margins on some specimens. Fifteen specimens.

Genus *Divaricella* von Martens 1880

Divaricella quadrisulcata Orbigny. Plate 8, Fig. 3A, 3B. Slightly less than 25 mm. Orbicular, well inflated. Cream colored, glossy. Sculpture of fine, criss-cross grooves. One specimen.

Divaricella dentata Wood. Plate 8, Fig. 1A, 1B. 25 to 37 mm. Orbicular, inflated. Color: cream. Sculpture of fine, criss-cross threads which extend beyond margins to form serrated edge; serration prominent on dorsal margin. 4 to 6 deeply impressed, concentric growth lines. Six specimens.

CHAMIDAE

Genus *Chama* Linnaeus 1758

Chama macerophylla Gmelin. Plate 6, Fig. 5A, 5B. 31 to 69 mm in height. Heavy, roughly oval in outline. Concentric sculpture of irregular, fimbriated or foliated lamellae. Inner valve margins crenulated. Colors: yellow, pale pink, lavender. Eight specimens.

CARDIIDAE

Genus *Trachycardium* Morch 1853

Trachycardium isocardia Linnaeus. 53 mm in height, 44 mm wide. One beach specimen, dull white with flecks of pale yellow. 32 rounded, radial ribs.

Genus *Trigoniocardia* Dall 1900

Trigoniocardia media Linnaeus. Plate 8, Fig. 10A, 10B. One specimen 31 mm high. Shell thick, inflated. Posterior slope descends sharply. 34 strong, radial ribs, bearing chevron-shaped scales. Margins serrated. Escutcheon and lunule not defined. White splotched with light purple.

Genus *Laevicardium* Swainson 1840

Laevicardium laevigatum Linnaeus. Plate 6, Fig. 1A, 1B. 31 to 40 mm in height, not as wide. Shell thin, well inflated, slightly oblique. Surface smooth except for microscopic sculpture. Glossy white with pink tinge near ligament; interior of some specimens flushed with pale yellow. Inner margins finely serrated. Six specimens.

VENERIDAE

Genus *Antigona* Schumacher 1817

Antigona listeri Gray. Plate 7, Fig. 6A, 6B. Slightly more than 75 mm. Thick, heavy, oblong-oval. Sculpture of numerous, low, radial riblets crossed by blade-like, serrated, concentric ridges. Gray-white with light brown splotches. Interior white, stained purplish-black on posterior third. Two specimens.

Antigona rigida Dillwyn. Plate 6, Fig. 3A, B. 62 mm, sub-circular in outline, inflated. White with long, chevon-shaped streaks of purplish brown. Sculpture of prominent, sharp, lamellate, concentric ridges; 1 to 4 concentric threads between ridges on upper half of valves. One specimen.

Genus *Chione* Mühlfeld 1811

Chione cancellata Linnaeus. Plate 8, Fig. 4. 25 mm in width, three-fourths as high. Low radial riblets crossed by sharp, blade-like, concentric ridges. Long, smooth escutcheon. Lunule heart-shaped with fine, vertical lines. Color: flat white, few irregular markings of dark brown and pink. Umbones pink. One specimen.

Petricolidae

Genus *Petricola* Lamarck 1801

Petricola lapicida Gmelin. Plate 9, Fig. 5A, 5B. 15 mm in height. Ovate, well inflated, grayish-white. Sculpture of minute, criss-cross threads. 5 to 7 irregular, wavy ribs on posterior end. Interior glossy white with pale green tinge. Three specimens.

Tellinidae

Genus *Tellina* Linnaeus 1758

Tellina interrupta Wood. Plate 7, Fig. 1A, 1B. 56 to 100 mm. Elongate, flattened, unpolished. Posterior end twisted. Sculpture of numerous, rough, evenly spaced, concentric threads. Color: white with zigzag markings of light brown. Five specimens.

Tellina radiata Linnaeus. Plate 7, Fig. 2A, 2B. 68 to 93 mm. Elongate. Porcelaneous. Shell creamy-white with broad rays of pinks and/or lavender. Interior all white or flushed with yellow. Beaks bright red. Three specimens.

Tellina candeana Orbigny. Plate 9, Fig. 4A, 4B. 12 to 15 mm. Moderately elongate, thin, fragile, translucent white. Sculpture of growth lines and numerous wavy, concentric threads which cross the shell at oblique angle. Twelve specimens.

Genus *Arcopagia* Brown 1827

Arcopagia fausta Pultney. Plate 7, Fig. 5A, 5B. 68 to 88 mm. Oval in outline, relatively heavy. Smooth, except for lines of growth. Color: white with faint sheen. Interior glazed, flushed with pale yellow. Two specimens.

Genus *Strigilla* Turton 1822

Strigilla mirabilis Philippi. Plate 9, Fig. 2A, 2B. 10 to 15 mm. Oval, moderately inflated, translucent white. Sculpture of fine, impressed, criss-crossed lines. Pallial line does not reach anterior muscle scar. Inner margins smooth. Six specimens.

Genus *Apolymetis* Salisbury 1929

Apolymetis intastriata Say. Plate 7, Fig. 3A, 3B. 63 mm. Oblong in outline. Dull white. Thin but strong. Posterior end twisted to the right. Strong radial ridge at posterior end of right valve, corresponding groove on left valve. Large pallial sinus. One specimen.

SCAPHOPODA

SIPHONODENTALIIDAE

Genus *Cadulus* Philippi 1844

Cadulus sp. Plate 3, Fig. 25. 19 mm, smooth. Apex with 4 well-defined notches. One specimen.

DENTALIIDAE

Genus *Dentalium* Linnaeus 1758

Dentalium sp. Plate 3, Fig. 2B. 23 mm, apex missing. White with apaque dots. Sculpture of numerous, low, flat ribs of varing widths. One specimen.

AMPHINEURA

ISCHNOCHITONIDAE

Genus *Ischnochiton* Gray 1847

Ischnochiton sp. Plate 9, Fig. 12A, B. Slightly less than 25 mm, elongate, narrow. Color: grayish-green, speckled with dark green and black. Girdle covered with minute scales. Lateral areas raised, with wavy, beaded, longtitudinal riblets. Central areas similarly sculptured. End valves concentrically beaded. Four specimens.

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PLATE 1

ALACRAN REEF GASTROPODS

2 to 3 times life size

Text reference

1A,B. *Diodora listeri* Orbigny 367
2A,B. *Lucapina philippiana* Finlay 367
3A,B. *Diodora minute* Lamarck 367
4A,B. *Lucapina suffusa* Reeve 367
5A,B. *Acmaea pustulata pulcherrima* Guilding 367
6A,B. *Acmaea jamaicensis* Gmelin 367
7A,B. *Hemitoma emarginata* de Blainville 367
8A,B. *Cheilea equestris* Linnaeus 372
9A,B. *Hipponix antiquatus* Linnaeus 372

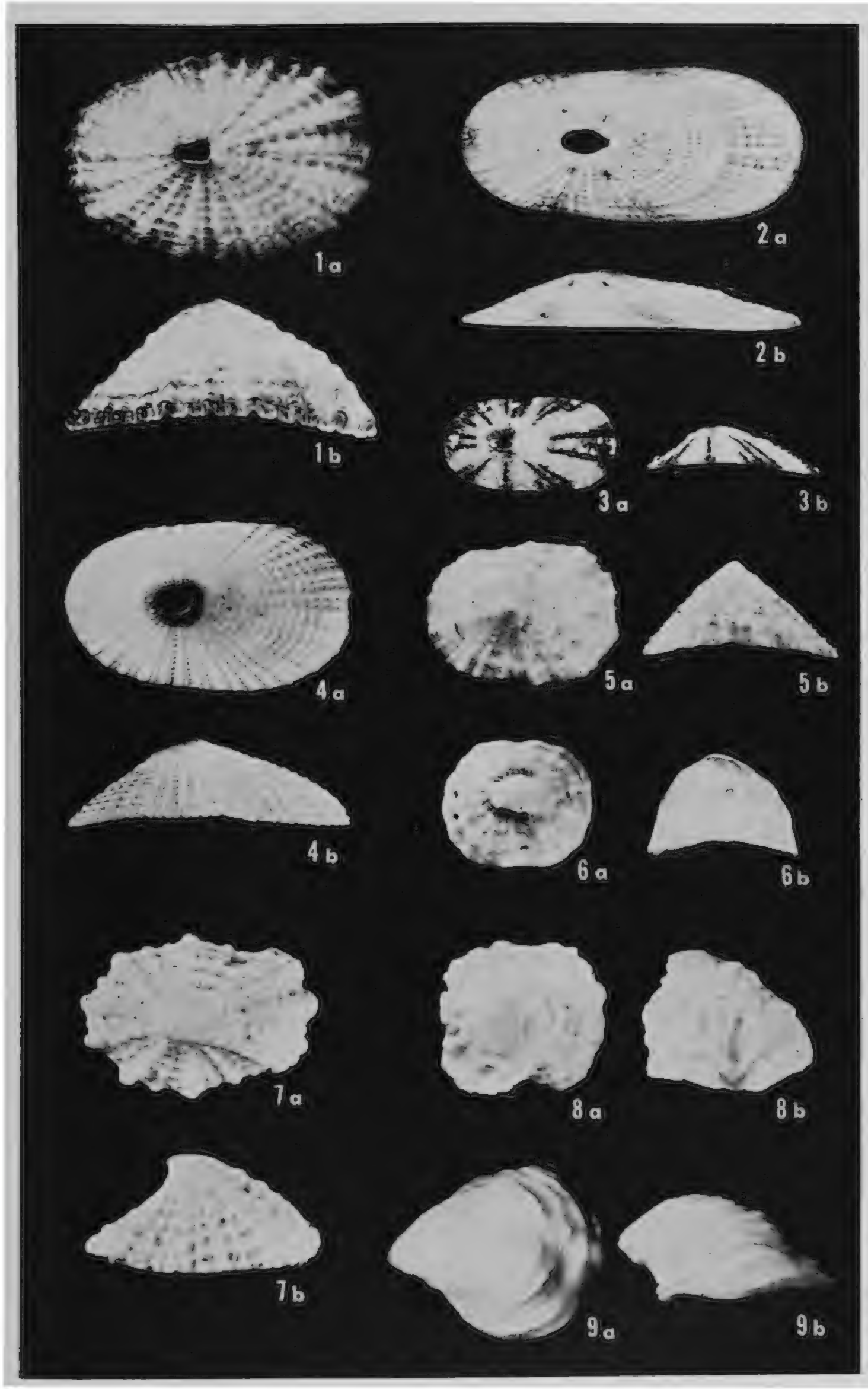


PLATE 1

PLATE 2

ALACRAN REEF GASTROPODS

life size

		Text reference
1.	*Cymatium gemmatum* Reeve	371
2.	*Cerithium literatum* Born	371
3.	*Conus mus* Hwass	377
4.	*Prunum labiatum* Valenciennes	377
5.	*Cyphoma gibbosum* Linnaeus, two views, A, B.	373
6.	*Calliostoma jujubinum* Gmelin	368
7.	*Calliostoma zonamestum* A. Adams	367
8.	*Nerita peloronta* Linnaeus	369
9.	*Nerita tessellata* Gmelin	369
10.	*Nerita versicolor* Gmelin	369
11, 12.	*Turbo cailletii* Fischer and Bernard	368
13.	*Thais deltoidea* Lamarck	375
14.	*Astraea americana* Gmelin	369
15.	*Cymatium caribbaeum* Clench and Turner	374
16, 17.	*Vermicularia knorri* Deshayes	370
18.	*Petaloconchus* cf. *nigricans* Dall, (x 2)	370

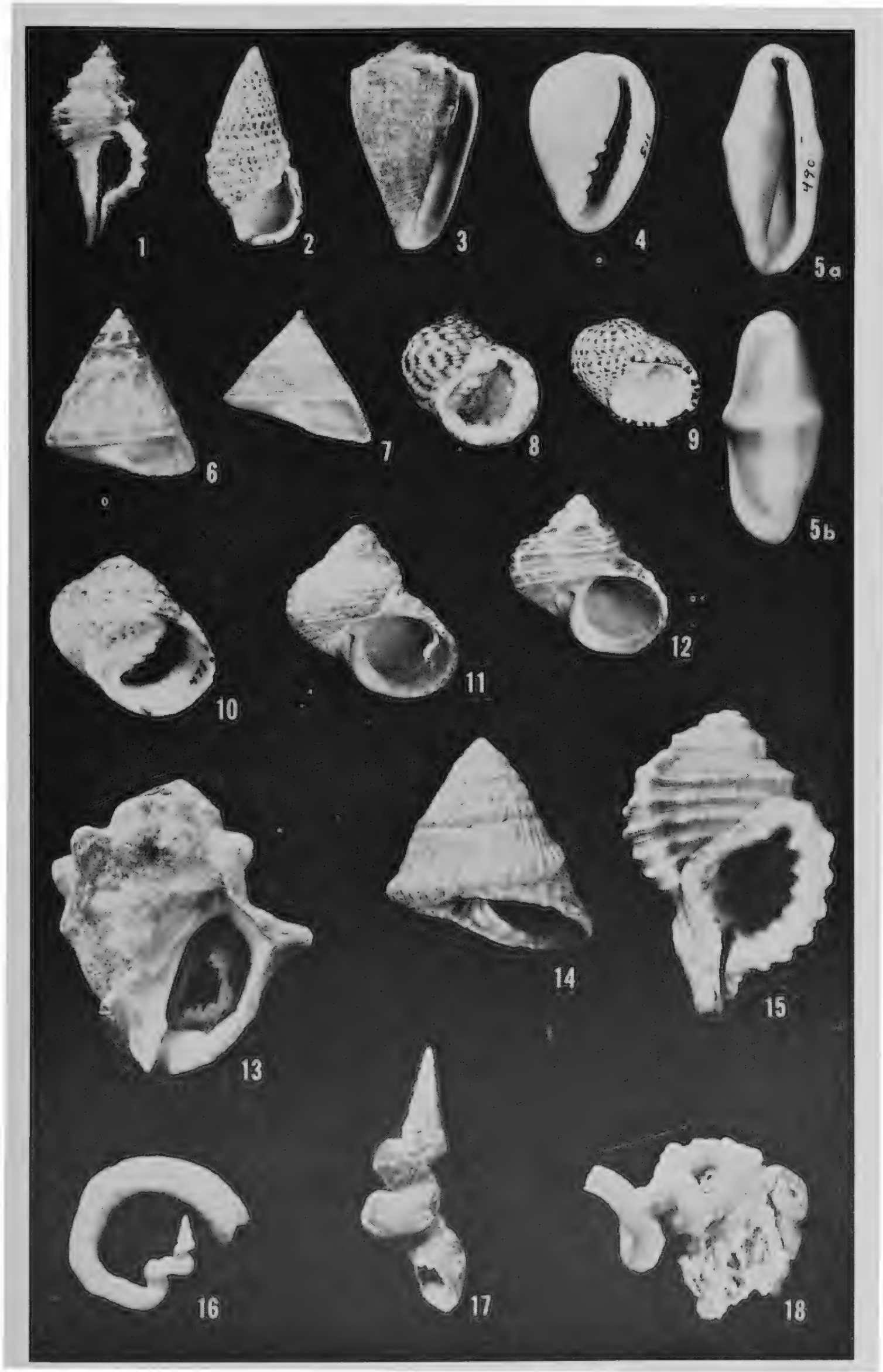


PLATE 2

PLATE 3

ALACRAN REEF GASTROPODS AND SCAPHOPODS

Text reference

1. *Prunum guttatum* Dillwyn (x 2) 377
2. *Bulla sp.* (x 2) 378
3. *Atys caribaea* Orbigny (x 2) 378
4. *Nodilittorina tuberculata* Menke (x 2) 370
5. *Drupa nodulosa* C. B. Adams (x 2) 374
6, and 8. *Littorina ziczac* Gmelin (x 2) 369
7. *Neritina virginea* Linnaeus (x 5) 369
9. *Batillaria minima* Gmelin (x 5) 371
10. *Cerithium algicola C. B. Adams* (x 2) 371
11. *Alaba sp.* (x 5) 371
12. *Seila adamsi* H. C. Lea (x 5) 371
13. *Rissoina cancellata* Philippi (x 5) 370
14. *Rissoina multicostata* C. B. Adams (x 5) 370
15. *Pusia gemmata* Sowerby (x 5) 377
16. *Rissoina chesneli* Michaud (x 10) 370
17. *Balcis sp.* (x 10) 372
18. *Odostomia sp.* (x 10) 378
19. *Tricolia* cf. *thalassicola* Robertson (x 5) 369
20. *Sinum perspectivum* Say (x 2) 373
21. *Cyclostrema cancellatum* Marryat (x 10) 368
22. *Caecum cooperi* S. Smith (x 10) 370
23. *Caecum floridanum* Stimpson (x 10) 370
24. *Caecum nebulosum* Rehder (x 10) 371
25. *Cadulus sp.* (x 10) 384
26. *Dentalium sp.* (x 10) 384

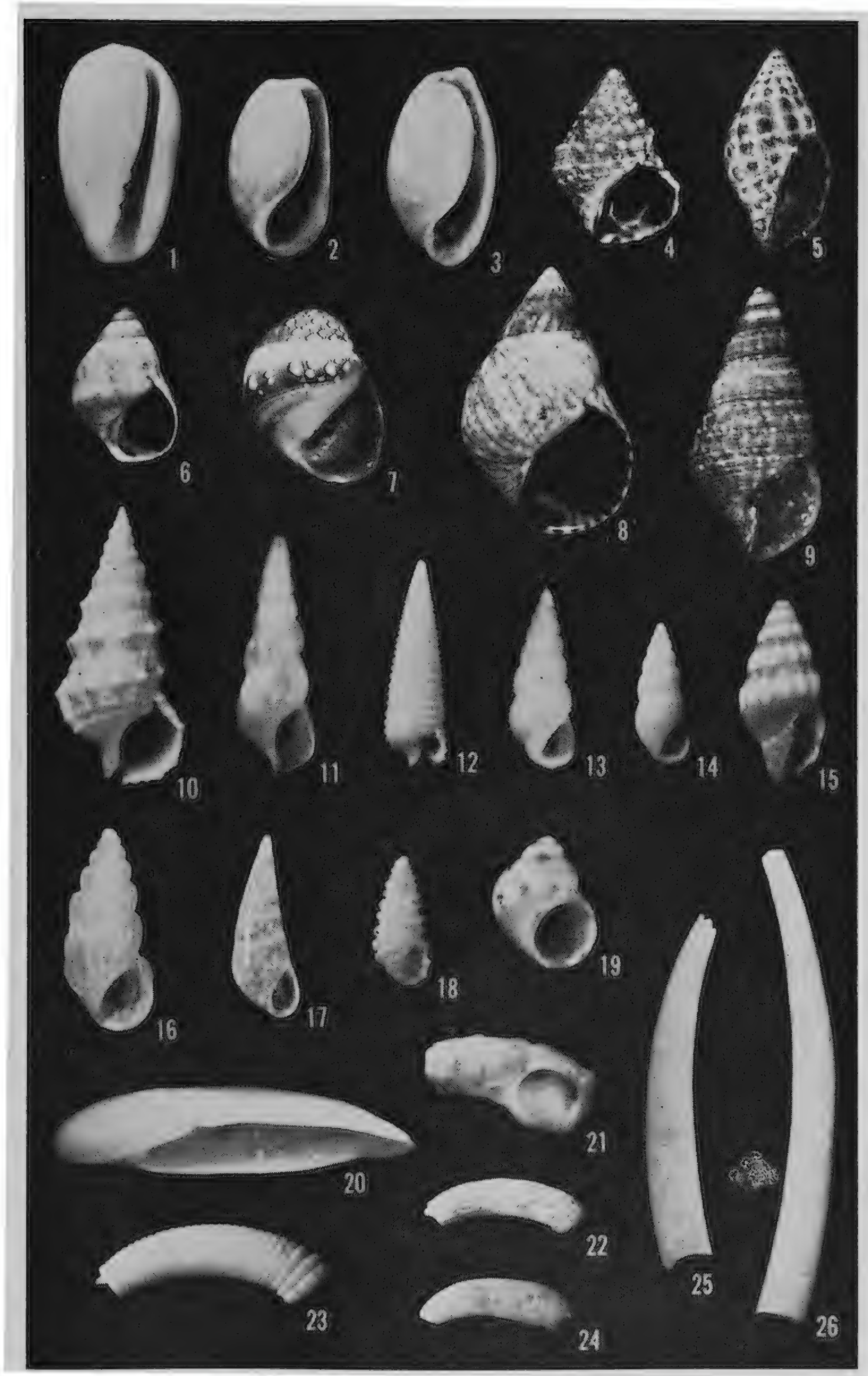


PLATE 3

PLATE 4

ALACRAN REEF GASTROPODS

3 times life size

Text reference

1. *Bailya intricata* Dall 375
2. *Nassarius ambiguus* Pulteney 376
3. *Cerithium variabile* C. B. Adams 371
4. *Triphora decorata* C. B. Adams 372
5. *Columbella mercatoria* Linnaeus 375
6. *Anachis pulchella* Sowerby 375
7. *Nitidella nitidula* Sowerby 375
8. *Hyalina avena* Valenciennes 375
9. *Olivella nivea* Gmelin 376
10. *Atys sandersoni* Dall 378
11. *Persicula sp.* 377
12. *Haminoea succinea* Conrad 378
13. *Smaragdia viridis* Linnaeus 369
14. *Batillaria minima* Gmelin 371
15. *Arene* cf. *cruentata* Muhlfeld 368
16. *Modulus modulus* Linnaeus 371
17. *Trivio suffusa* Gray 373
18. *Calliostoma sp.* 368
19. *Epitonium sp.* 372
20. *Cerithium eburneum* Bruguiere 371

PLATE 4

PLATE 5

ALACRAN REEF GASTROPODS

½ to ⅔ life size

Text reference

1, 2. *Strombus gigas* Linne (x ½) 372
3. *Xancus angulatus* Solander (x ½) 376
4, 8. *Fasciolaria tulipa* Linnaeus (x ½) 376
5, 10. *Strombus raninus* Gmelin (x ½) 373
6, 9. *Strombus costatus* Gmelin (x ½) 372
7. *Busycon spiratum* Lamarck (x ½) 376
11, 16. *Tonna galea* Linnaeus (x ⅓) 374
12. *Busycon contrarium* Conrad (x ½) 375
13. *Tonna maculosa* Dillwyn (x ½) 374
14. *Leucozonia nassa* Gmelin (x ⅔) 376
15. *Natica canrena* Linnaeus (x ⅔) 373
17. *Astraea caelata* Gmelin (x ⅔) 369
18. *Astraea longispina* Lamarck (x ⅔) 368
19. *Cymatium pileare* Linnaeus (x ⅔) 374

PLATE 5

PLATE 6

ALACRAN REEF PELECYPODS

½ to ⅔ life size

Text reference

1A,B. *Laevicardium laevigatum* Linnaeus (x ⅔) 382

2A,B. *Codakia orbicularis* Linnaeus (x ⅔) 381

3A,B. *Antigona rigida* Dillwyn (x ½) 382

4A,B,C. *Ostrea frons* Linnaeus (x ⅔) 381

5A,B. *Chama macerophylla* Gmelin (x ⅔) 382

6A,B. *Pinctada radiata* Leach (x ⅔) 380

7A,B. *Arca umbonata* Lamarck (x ⅔) 378

8A,B. *Arca zebra* Swainson (x ⅔) 378

9. *Pinctada radiata* Leach (x ⅔) 380

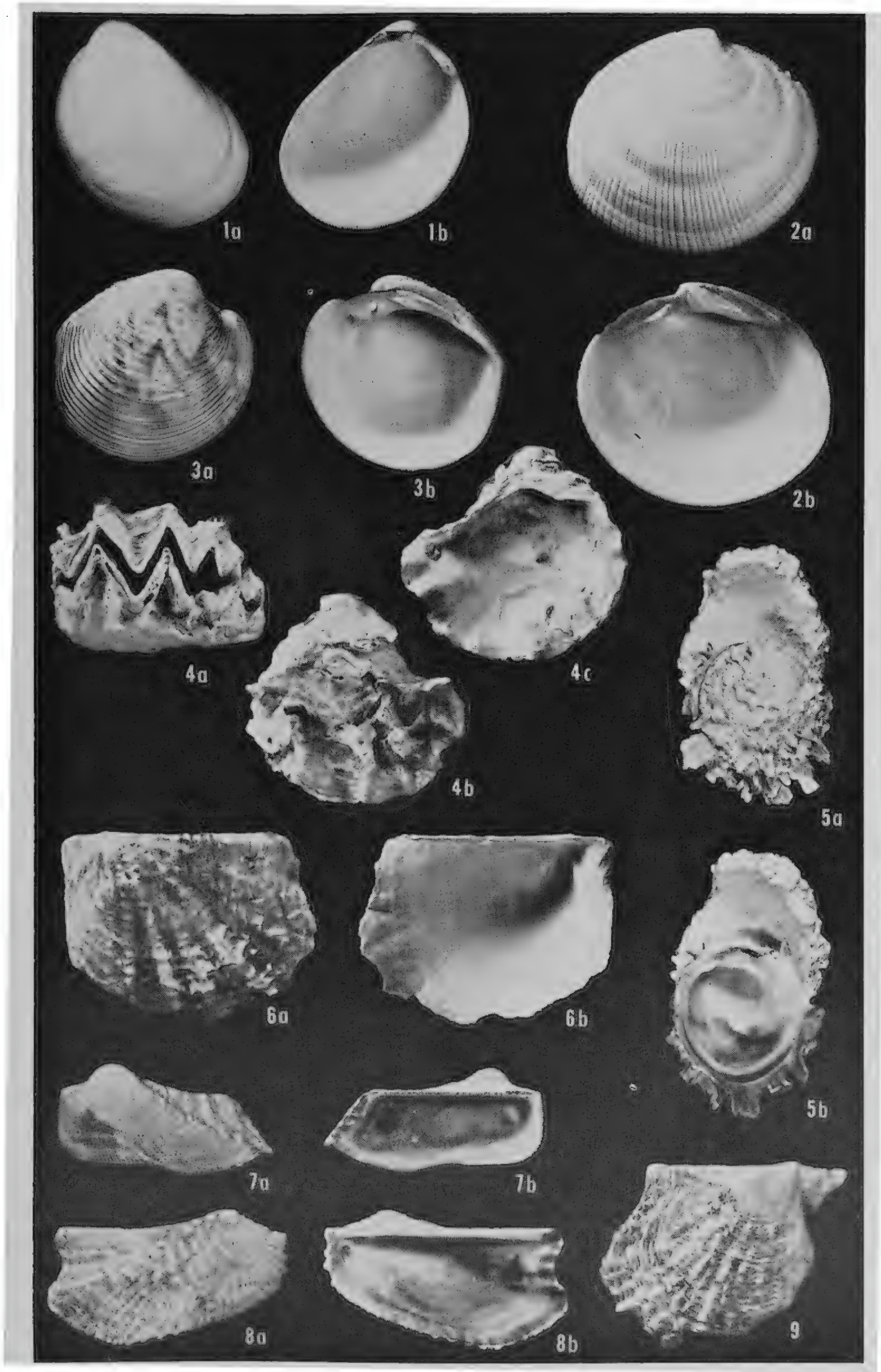


Plate 6

Plate 7

ALACRAN REEF PELECYPODS

½ to ⅔ life size

Text reference

1A,B. *Tellina interrupta* Wood (x ⅔) 383

2A,B. *Tellina radiata* Linnaeus (x½) 383

3A,B. *Apolymetis intastriata* Say (x ⅔) 383

4A,B. *Lima scabra* Born (x ½) 381

5A,B. *Arcopagia fausta* Pulteney (x ½) 383

6A,B. *Antigona listeri* Gray (x ½) 382

7A,B. *Modiolus americanus* Leach (x ⅔) 379

8A,B. *Lithophaga nigra* Orbigny (x ⅔) 379

PLATE 7

PLATE 8

ALACRAN REEF PELECYPODS

life size

Text reference

1A,B. *Divaricella dentata* Wood 382

2. *Chlamys imbricata* Gmelin, upper valve 380

3A,B. *Divaricella quadrisulcata* Orbigny 382

4. *Chione cancellata* Linnaeus 383

5. *Chlamys imbricata* Gmelin, (½ life size) interior, lower valve 380

6A,B. *Lucina pensylvanica* Linnaeus 381

7A,B. *Lyropecten antillarum* Recluz 380

8A,B. *Lima lima* Linnaeus 381

9A,B. *Spondylus americanus* Hermann, upper valve, exterior, interior 380

10A,B. *Trigoniocardia media* Linnaeus 382

11. *Ostrea frons* Linnaeus, interior, attached valve 381

12A,B. *Barbatia cancellaria* Lamarck 379

13. *Brachidontes citrinus* Röding 379

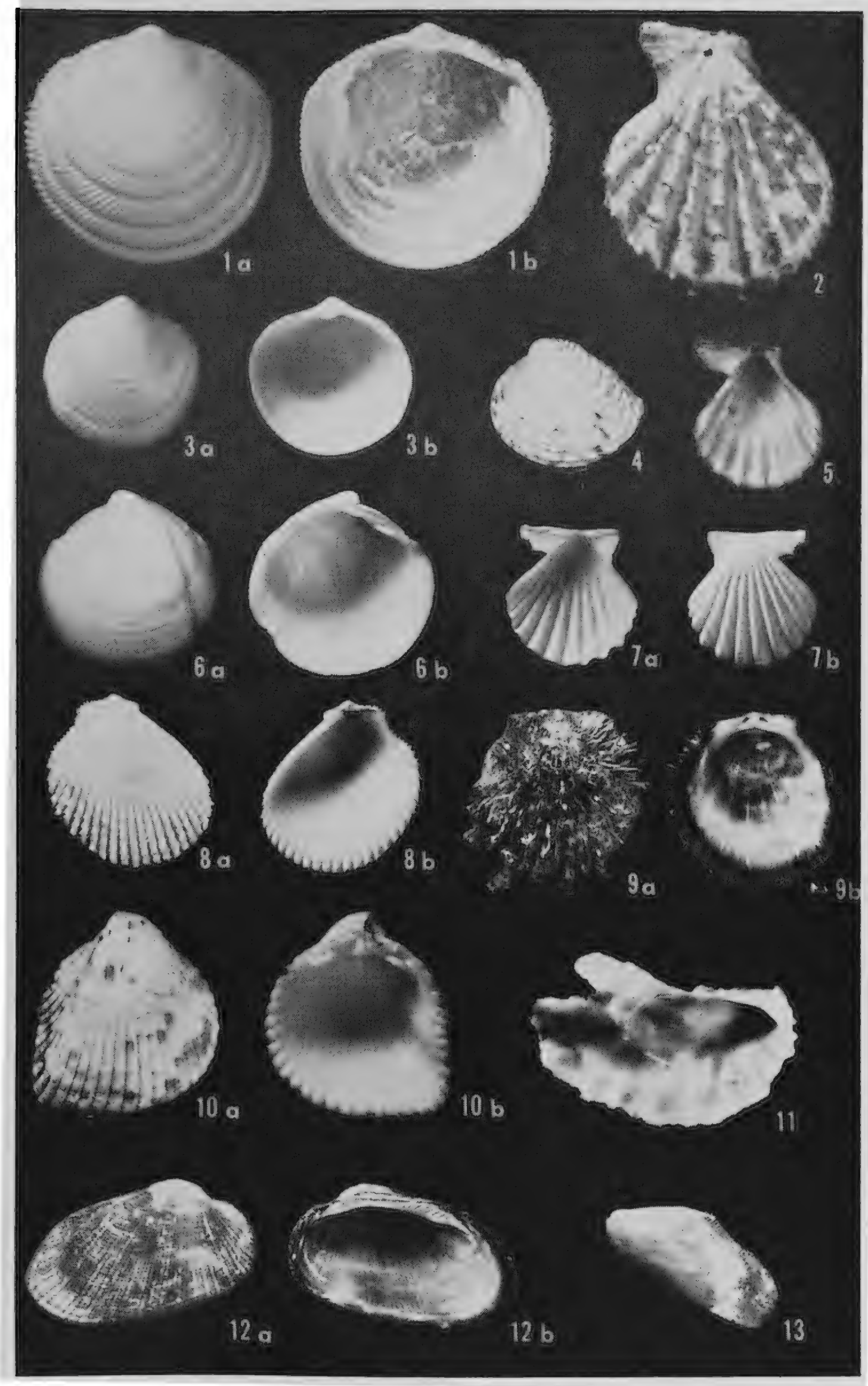


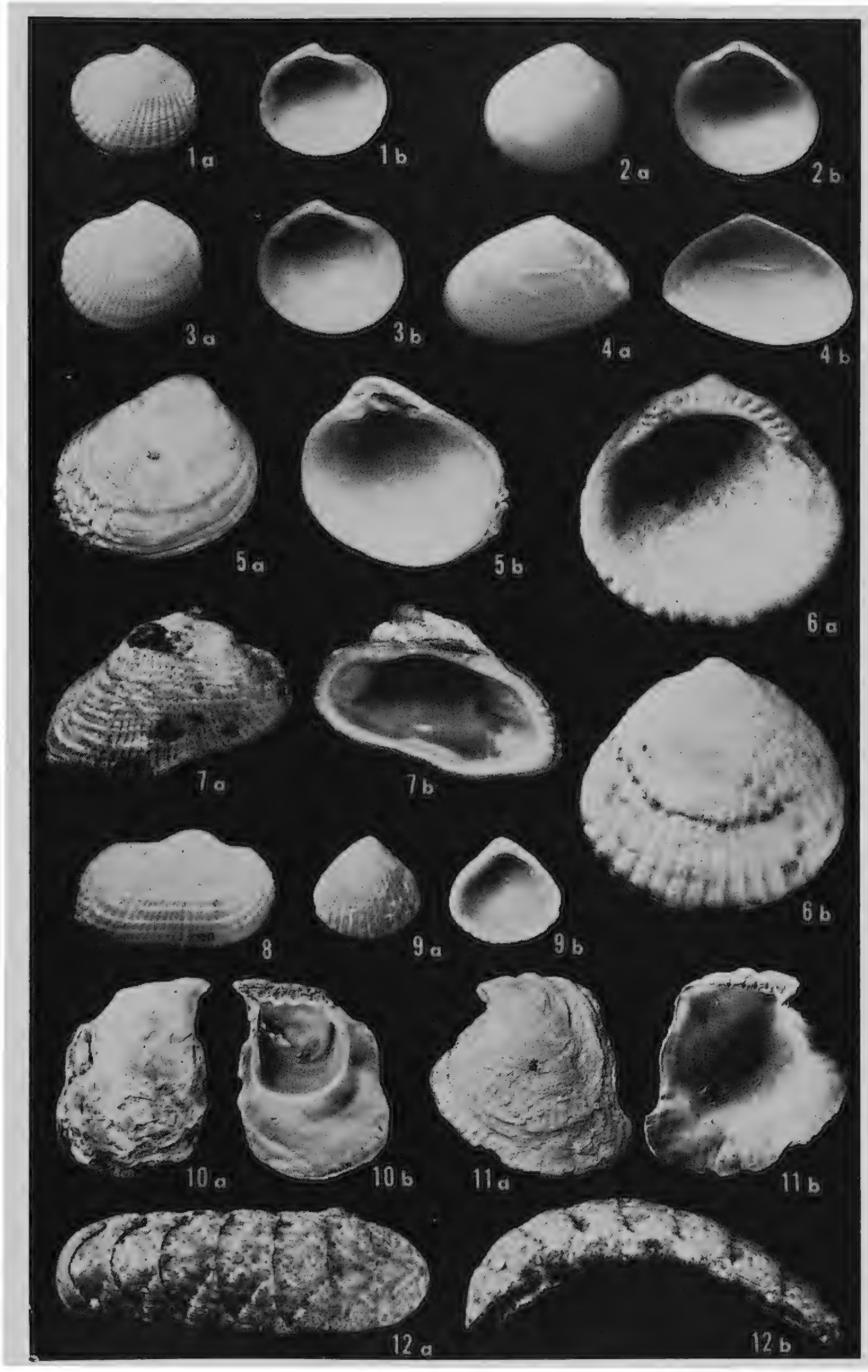
PLATE 8

PLATE 9

ALACRAN REEF PELECYPODS

Text reference

1A,B. *Codakia* cf. *orbiculata* Montagu (x 2) 381
2A,B. *Strigilla mirabilis* Philippi (x 2) 383
3A,B. *Codakia* cf. *orbiculata* Montagu (x 2), (variation ?) 381
4A,B. *Tellina candeana* Orbigny (x 2) 383
5A,B. *Petricola lapicida* Gmelin (x 2) 383
6A,B. *Glycymeris pectinata* Gmelin (x 2) 379
7A,B. *Barbatia domingensis* Lamarck (x 2) 379
8. *Arcopsis adamsi* E. A. Smith (x 5) 379
9A,B. *Venericardia sp.* (x 5) 381
10A,B. *Isognomon* cf. *bicolor* C. B. Adams (x 2) 380
11A,B. *Isognomon alatus* Gmelin (life size) 379
12A,B. *Ischnochiton sp.* (x 3) 384


1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b
7a
7b
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9a
9b
10a
10b
11a
11b
12a
12b

PLATE 9

Chronological Record of Contributions From the Institute of Marine Science 1945–1960

Publications by staff, students, and visiting investigators. An asterisk (*) indicates co-authors associated with the Institute.

1945

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1947

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1949

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